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Proceedings of the International Workshop on Snow Crab Biology, December 8-10, 1987, Montréal, Québec

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PROCEEDINGS OF THE INTERNATIONAL WORKSHOP ON SNOW CRAB BIOLOGY, DECEMBER 8-10, 1987, MONTREAL, QUEBEC

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We express our thanks to all the speakers, rapporteurs, and participants who contributed so substantially to the success of this report. This report summarizes presentations made at the meeting, but unfortunately, the full texts of all presentations could not be included in this volume. We acknowledge the unpublished presentations led by M. Sinclair, R. W. Elner, G. Charmentier, A. Boghen, and R. Bailey.

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ABSTRACT

Jamieson G.S., and W.D. McKone (ed.). 1988. Proceedings of the International Workshop on Snow Crab Biology, December 8-10, 1987, Montreal, Quebec. Can. MS Rep. Fish. Aquat. Sci. 2005: 163 p.

The proceedings of a Workshop on Snow Crab Biology are presented. Objectives of the Workshop were to review the current understanding of snow crab biology, to evaluate the implications of recent advances in our understanding of snow crab biology on the management of the resource, and to present recommendations as to the direction of future biological research on snow crab. Consensus among participants was achieved for the following points: the five, existing management units for snow crab in Atlantic Canada are biologically acceptable; both male and female Chionoecetes opilio in eastern Canada are now considered to have a terminal moult, although the size at which this may occur is variable; and while males can commence spermatogenesis as small as 40 mm carapace width (CW), whether such males are functionally capable of copulation remains uncertain.

It was recognized that the seasonal timing of fishing in each management unit has not necessarily been set on the basis of biology except to avoid a preponderance of white (soft-shell) crab in the catch, that the current legal size of 95 mm (CW) is not based on biological advice, and that the increasing proportion of white crabs in the catch may be partially the result of the changing proportions of preterminal and terminal moult male crabs in the population. With respect to future research, there was consensus that the greatest need was to establish growth rate, the factors influencing when a crab undergoes a terminal moult, and the natural mortality and longevity of terminal moult males.

RÉSUMÉ

Jamieson G.S., and W.D. McKone (ed.). 1988. Proceedings of the International Workshop on Snow Crab Biology, December 8-10, 1987, Montreal, Quebec. Can. MS Rep. Fish. Aquat. Sci. 2005: 163 p.

On présente le compte rendu d'un atelier portant sur la biologie du crabe des neiges. Les objectifs de cet atelier étaient les suivants: passer en revue les connaissances actuelles sur la biologie du crabe des neiges; evaluer les incidences sur la gestion de la ressource des nouvelles connaissances acquise relativement à la biologie du crabe des neiges et presenter des recommandations sur l'orientation des recherches biologiques à venir sur le crabe des neiges. Les participants se sont entendus sur les points suivants: les cinq unités de gestion du crabe des neiges sur la côte atlantique du Canada sont acceptable du point de vue biologique; les crabes *Chionoecetes opilio* tant mâles que femelles de l'Est du Canada sont considérés maintenant comme ayant une mue terminale, bien que la taille à laquelle cela peut ce traduire soit variable; finalement, bien que la spermatogénèse puisse commencer chez les mâles dès que la largeur de la carapace (LC) atteint 40 mm, on n'est pas sûr que ces mâles soient fonctionnellement capables de s'accoupler.

On a reconnue que la saison de pêche dans chaque unité de gestion n'a pas été nécessairement en fonction de la biologie de l'espèce, sauf pour éviter qu'il y ait prépondérance de crabes blancs (à carapace molle) dans les prises; que la taille légal actuelle de 95 mm (LC) n'est pas basée sur une recommandation biologique et que la proportion croissante de crabes blancs dans les prises pourrait être due en partie au changement dans les proportions de crabes mâles en mue préterminale et en mue terminale dans la population. En ce qui concerne les recherches à venir, on a convenu qu'il faillait surtout déterminer le rythme de croissance, les facteurs ayant une influence lorsqu'un crabe subit un mue terminale de même que la mortalité naturelle et la longévité des mâles en mue terminale.

EXECUTIVE SUMMARY

by

G.S. Jamieson, R. Bailey, G.Y. Conan, R.W. Elner,
W.D. McKone, and D.M. Taylor

The Workshop on the biology of snow crab was organized in response to a request by the Assistant Deputy Minister, Science, Dr. L. S. Parsons. The meeting was convened in early December, 1987, so that the findings would be available for program planning for 1988/89 and the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) assessment meeting in early January, 1988. Concerns included: past over-exploitation of the resource, a change in the seasonal moulting pattern of crab ahead of previous seasons, and the slow start-up of the fishery because of cold water temperatures or unusual ice conditions. Some aspects of these points will be addressed within CAFSAC as they are beyond the mandate of the Workshop.

The objectives of the meeting were as follows:

1) To review our current understanding of snow crab biology, with emphasis on recent advances.

2) To evaluate the implications of these biological advances on the management of the resource in the context of both current and alternate management scenarios.

3) To present recommendations as to the direction of future biological research on snow crab, and to develop a general strategy on how this can best be achieved.

Participants included federal, provincial and university researchers working on snow crab in Canada as well as experts on crab biology from the U.S., U.K. and France.

The immediate issues which precipitated the meeting were:

1) A provisional estimated decline in total landings from the southwestern Gulf of 51% between 1985 and 1987.

	Landings					
	Gulf			Quebec	Scotia-Fundy	Newfoundland
Year	Southwest	Cape Breton	PEI	North Shore	Cape Breton	
1985	25258	1764	801	5818	84	7598
1987	12340	1769	458	4823	361	6837

2) Scientific debate as to whether there was a terminal moult or continuous growth in snow crab, and the resulting significance to exploitation level and management.

3) Scientific debate as to the size at which male snow crab become sexually mature and capable of copulation with either primiparous (virgin) or multiparous females, and the resulting appropriateness of existing management regulations.

Consensus was achieved on the following points:

Management Units:	The five existing management units for snow crab in Atlantic Canada (Southwestern Gulf, north shore of Québec, Cape Breton, and northern and southern Newfoundland) are biologically acceptable, since movement after larval settlement is largely restricted (< 25km).
Terminal Moult:	Male and female Chionoecetes opilio in eastern Canada are now considered to have a terminal moult. The size, and presumably age, at which this may occur is variable. What factors influence when an individual crab undergoes its terminal moult are unknown, but for males, the terminal moult may be reached at any size between 50-150 mm carapace width (CW). The current legally harvestable minimum size limit is 95 mm CW. It is unclear whether this variable size at terminal moult also exists for C. opilio in the Bering Sea or for other Chionoecetes species.
Sexual Maturity:	Most males can commence spermatogenesis as small as 40 mm CW, i.e. potentially a number of moults before their terminal moult. Whether such preterminal males can copulate has not been established, and there is also debate as to whether small terminal moult males (< 95 mm CW) can copulate with multiparous (i.e. hard-shelled) females.

The implications of these biological features on resource management could not be fully established at this time because of gaps in our understanding of snow crab biology. The basis behind existing regulations is as follows:

Timing of Fishing:

Moulting, mating, egg hatching and spawning all occur in the spring, coinciding with the current fishing period in the southwest Gulf. Occurrence of white, i.e. soft-shell, crab is delayed until summer in Newfoundland and in some areas in the Gulf. The timing of the fishing season in each management unit has not necessarily been set on the basis of biology except to avoid a preponderance of white crab in the catch.

Minimum Legal Size:

The current legal size of 95 mm CW is not based on biological criteria. The full appropriateness of the existing regulation is uncertain for 1) maximizing yield per recruit, because little is known about what determines the size at which a male undergoes its terminal moult, and 2) for avoiding recruitment overfishing, because, similarly, there is no consensus about the concurrence of the onset of maturity with the terminal moult of males. There is no evidence to date of recruitment overfishing because females are not exploited and most appear to be carrying eggs. However, non-mated females may carry non-fertile broods for extensive periods after spawning.

White Crab (Soft-shell):

The white crab problem is largely the result of two issues. As the number of large terminal males in the population decreases because of the fishery, then 1) the proportion of recently moulted males in the population increases, resulting in "apparent" higher abundance of white crab males in the catch, and 2) disappearance of terminal males may actively induce recruitment of preterminal sublegal males to the fishery. In a fully exploited population, a steady state may be achieved, but it is unclear as to whether this can occur, or is indeed desirable for any snow crab stock. When the proportion of recruiting crab in the catch is high, meat yield and quality are reduced.

General Recommendations:

To allow development of improved biological advice for management, the following research, and its priority, was agreed to by all participants. There was consensus that the greatest need was to establish growth rate, the factors influencing when an animal undergoes a terminal moult, and the natural mortality and longevity of terminal males. Monitoring of these factors should be conducted by departmental at-sea sampling.

Secondarily, the longer-term impact of the present management strategy on population fecundity needs investigation. Specifically, the relative contribution of small terminal males (< 95 mm CW), large terminal males (> 95 mm CW) and preterminal males to reproduction requires resolution.

The priority of each of the following specific recommendations identified during the meeting is the average of those given by Workshop Steering Committee members.

SPECIFIC RESEARCH RECOMMENDATIONS	Priority
Determine:	(1=high, 2=moderate)
1) Stock definition and movement:	
- electrophoretic and other biochemical characteristics of larvae and adults from each management unit;	2
- larval distribution and survival in relation to oceanographic characteristics;	2

	Priority (1=high, 2=moderate)
- movement of crabs in relation to location, time at large and season. These could include ultra-sonic telemetry.	1.8
2) Growth:	
- the precise morphometric relationship between chelae and carapace sizes for all snow crab stocks;	1.5
- growth increment and frequency of moulting at size and age for each management unit year round;	1
- the factors affecting incidence of normal terminal moulting in snow crabs year round.	1
3) Reproductive Behaviour:	
- the reproductive contribution of both preterminal moult male crabs and sublegal size, terminal moult crabs relative to both primiparous and multiparous females.	1.6
- the proportion of fertilized versus nonfertilized, and eyed, egg masses observed in the field;	1
- annual female egg production, including examination of spermathecal contents and gonadal condition.	1
4) Natural Mortality:	
- natural mortality at size within each management unit, including study of egg retention until hatching.	2
5) Management:	
- have an experimental fishery where males at a small terminal size are fished heavily to establish stock response, i.e.:	2
a) to determine if there is increased growth rate and earlier recruitment of small males to the fishery;	
b) to determine if there is reduced mortality of prerecruit preterminal males.	
c) to determine the effect on fertilized egg production;	

	Priority (1=high, 2=moderate)
- explore the implications of 1) pulse and rotational fishing, and 2) of using a chelae measurement in a minimum size regulation.	1.5
6) Population Assessment:	
- precision and accuracy of catch and effort reporting should be improved, including documentation of temporal fishing patterns, fishing location, soak time, etc.	1.2
- establish annual prerecruit abundance and survival;	1
- develop yield per recruit models;	1.6
- monitor at-sea undersize crabs caught in the commercial fishery, shell condition, moult stages, and morphometrics of the entire size range of the catch.	1.2

RÉSUMÉ D'ORIENTATION

par

G.S. Jamieson, R. Bailey, G.Y. Conan, R.W. Elner,
W.D. McKone, et D.M. Taylor

L'atelier de travail sur la biologie du crabe des neiges fait suite à la demande de L.S. Parson présentée dans la note de service du 17 juillet 1987. La réunion a eu lieu au début de décembre afin que les résultats soient disponibles pour la planification des programmes de 1988-1989 et la réunion du CSCPCA qui aura lieu au début de janvier. Les problèmes étudiés sont les suivants : surexploitation passée de la ressource, la mue précoce du crabe par rapport aux années précédentes et le lent démarrage de la pêche à cause de la température froide de l'eau ou du régime extraordinaire des glaces. Certains aspects de ces problèmes seront étudiés par le CSCPCA car ils ne s'inscrivent pas dans le cadre du mandat de l'atelier de travail.

Les objectifs de la réunion sont les suivants :

1) Établir les connaissances actuelles sur la biologie du crabe des neiges surtout pour ce qui est des progrès récents;

2) Évaluer les conséquences de ces progrès biologiques sur la gestion de la ressource dans le contexte de scénarios de gestion actuels et autres; et

3) Présenter des recommandations sur l'orientation de la recherche future sur la biologie du crabe des neiges et élaborer une stratégie générale sur la meilleure façon de réaliser cet objectif.

Les participants comprennent des chercheurs oeuvrant au sein du gouvernement fédéral, des gouvernements provinciaux et d'universités qui effectuent des travaux sur le crabe des neiges au Canada ainsi que des spécialistes sur la biologie du crabe venant des États-Unis, du Royaume-Uni et de la France.

Les questions pressantes qui ont précité la présente réunion sont les suivantes :

1) Une prévision d'une chute de 51 % des débarquements totaux de la pêche dans le sud-ouest du golfe de 1985 à 1987.

	Débarquements					
	Golfe			Québec	Scotia-Fundy	Terre-Neuve
Année	Sud-ouest	Cap-Breton	Î.-P.-É.	Côte-Nord	Cap-Breton	
1985	25258	1764	801	5818	84	7598
1987	12340	1769	458	4823	361	6837

2) Une controverse scientifique quant à l'existence d'une mue terminale ou d'une croissance ininterrompue chez le crabe des neiges et la portée de ces facteurs sur le niveau d'exploitation et la gestion; et

3) Une controverse scientifique quant à la taille à laquelle les mâles atteignent la maturité sexuelle et sont capables de s'accoupler à des femelles primipares ou multipares et l'applicabilité des dispositions actuelles relatives à la gestion.

On a atteint l'unanimité sur les points suivants :

Secteurs de gestion : Les cinq grands secteurs de gestion du crabe des neiges de l'Atlantique canadien (sud-ouest du golfe, Côte Nord du Québec, Cap-Breton, nord de Terre-Neuve et sud de Terre-Neuve) sont acceptables au niveau biologique étant donné que les migrations après le début de la phase benthique sont dans une large mesure restreintes (<25 km).

Mue terminale : Il est maintenant accepté que les mâles et les femelles de *Chionoecetes opilio* de l'est du Canada connaissent une mue terminale. La taille, et vraisemblablement l'âge, à laquelle cette mue a lieu varie. On connaît mal les facteurs qui influent sur le moment de cette mue terminale mais chez les mâles, elle a lieu quand la carapace atteint une largeur (LC) de 50 à 150 mm.
À l'heure actuelle, la taille minimale légale se situe à 95 mm LC. On ne sait pas si cette variation de la taille à la mue terminale existe aussi dans le cas de *C. opilio* de la mer de Béring ou d'autres espèces de *Chionoecetes*.

Maturité sexuelle : Chez la plupart des mâles, la spermatogénèse peut avoir lieu dès que l'animal a atteint 40 mm LC soit quand il reste en principe un certain nombre de mues avant la mue terminale. On n'a pas déterminé si ces mâles peuvent s'accoupler ou si les mâles de petite taille (<95 mm LC) peuvent s'accoupler à des femelles multipares (c.-à-d. à carapace dure) après la mue terminale.

Il a été impossible d'établir les conséquences de ces facteurs biologiques sur la gestion de la ressources étant donné les lacunes de notre compréhension de la biologie du crabe des neiges. La réglementation actuelle est basée sur les points suivants :

Saison de pêche :

La mue, l'accouplement, l'éclosion des oeufs et la fraie ont lieu au printemps et coïncident avec la saison de pêche actuelle dans le sud-ouest du golfe. La mue n'a lieu qu'à l'été dans les eaux de Terre-Neuve et dans certaines régions du golfe. L'ouverture de la saison de pêche dans chaque secteur de gestion n'a pas forcément été fixée en fonction de facteurs biologiques sauf pour ce qui est de la fréquence de crabes à carapace molle dans les prises.

Taille légale minimale :

La taille légale minimale de 95 mm LC n'est pas basée sur des critères biologiques. L'applicabilité de la réglementation actuelle est douteuse dans les cas suivants : 1) la maximisation du rendement par recrue étant donné que l'on connaît mal les facteurs qui déterminent la taille à laquelle la dernière mue a lieu chez le mâle et 2) l'élimination de la surpêche au détriment du recrutement étant donné qu'il n'est pas définitivement établi si le début de la maturité coïncide à la dernière mue chez les mâles. Jusqu'à maintenant, aucune donnée ne porte à croire qu'il existe une surpêche au détriment du recrutement car les femelles ne sont pas exploitées et la plupart semblent porter des oeufs. Toutefois, les femelles non inséminées peuvent porter des oeufs non fertiles pendant de longues périodes après l'accouplement.

Crabe à carapace molle :

Le problème posé par les crabes à carapace molle est en grande partie le résultat de deux facteurs. Une baisse du nombre de gros mâles en phase terminale dans la population par suite de l'exploitation signifie que 1) le nombre relatif de mâles qui ont récemment mué augmente, ce qui entraîne une abondance "apparente" plus élevée de mâles à carapace molle dans les prises et 2) la disparition des mâles en phase terminale peut activement provoquer le recrutement à la pêche de mâles en phase préterminale de taille inférieure à la taille légale. Dans une population pleinement exploitée, un équilibre peut être atteint mais il n'est pas évident si ceci a eu lieu, peut être atteint ou est effectivement avantageux pour un stock de crabe des neiges. Quand le nombre relatif de crabes qui ont rallié le stock exploitable est élevé dans les prises, on observe une baisse du rendement en chair et de la qualité.

Recommandations générales :

Afin de permettre la prestation de conseils biologiques améliorés pour la gestion, les participants ont approuvé la réalisation des recherches suivantes en ordre de priorité. La détermination du taux de croissance, des facteurs qui influent sur le moment de la dernière mue, de la longévité et du taux de mortalité naturelle des mâles en phase terminale a fait l'objet d'un accord unanime comme priorités de recherche. Des échantillonnages en mer effectués par le personnel du Ministère devraient faire partie de l'étude de ces facteurs.

En deuxième lieu, l'incidence à long terme de la stratégie de gestion actuelle sur la fécondité de la population doit être étudiée. Plus précisément, la contribution relative des petits mâles en phase terminale (< 95 mm LC), des gros mâles en phase terminale (>95 mm LC) et des mâles en phase préterminale à la reproduction doit être établie.

La priorité que porte chacune des recommandations suivantes identifiées au cours de la réunion est la moyenne des cotes données par les membres du Comité de direction de l'atelier de travail.

RECOMMANDATIONS DE RECHERCHE PONCTUELLE	Priorité (1=élevée; 2=modérée)
1) Délimitation et migration des stocks :	
- caractéristiques électrophorétiques et autres particularités biochimiques des larves et des adultes dans chaque secteur de gestion;	2
- répartition et taux de survie des larves en fonction de facteurs océanographiques;	2
- migration des crabes en fonction de l'endroit fréquenté, de la durée de la période de déplacement et de la saison, peut-être par télémétrie par ultra-sons.	1.8
2) Croissance :	
- la relation morphométrique précise entre la taille des chélipèdes et la largeur de la carapace chez tous les stocks de crabe des neiges;	1.5
- les incréments de croissance et la fréquence de la mue selon la taille et l'âge pendant toute l'année dans chaque secteur de gestion;	1
- les facteurs qui influent pendant toute l'année sur l'incidence de la mue terminale normale chez le crabe des neiges.	1

	Priorité (1=élevée; 2=modérée)
3) Reproduction :	
- l'apport à la reproduction des mâles en phase préterminale et ceux en phase terminale de taille sublégale par rapport à l'apport des femelles primipares et multipares;	1.6
- le nombre relatif d'oeufs embryonnés fertilisés par rapport à ceux non fertilisés observés sur le terrain;	1
- la production annuelle d'oeufs y compris l'examen du contenu des spermatothèques et de la condition des gonades.	1
4) Mortalité naturelle :	
- le taux de mortalité naturelle selon la taille dans chaque secteur de gestion y compris l'étude de la rétention des oeufs jusqu'à l'éclosion.	2
5) Gestion :	
- la réalisation d'une pêche expérimentale où les mâles de petite taille en phase terminale seront fortement exploités afin de déterminer la réaction du stock, c.-à-d. : a) déterminer si le taux de croissance augmente et si le recrutement des mâles de petite taille à la pêche a lieu plus tôt; b) déterminer si le taux de mortalité des mâles prérecrutés en phase préterminale diminue; c) déterminer l'incidence sur la production d'oeufs fertilisés;	2
- l'étude des répercussions de 1) la pêche intermittente et rotative, et 2) l'utilisation de la longueur des chélipèdes dans une réglementation fixant une taille minimale.	1.5
6) Évaluation des populations :	
- l'exactitude et la précision des rapports sur les prises et l'effort devraient être améliorées notamment par l'inclusion des régimes temporels de pêche, le lieu de pêche, la durée de mouillage des engins, etc.;	1.2

	Priorité (1=élevée; 2=modérée)
- la détermination de l'abondance et de la survie annuelle des prérecrues;	1
- l'élaboration de modèles du rendement par recrue;	1.6
- l'observation en mer du nombre de crabes de taille inférieure à la taille légale capturés par les pêcheurs commerciaux, de la condition de la carapace, du stade de mue et des caractères morphométriques des crabes de toute taille capturés.	1.2

I. WORKSHOP REPORT

by

G.S. Jamieson, R. Bailey, G.Y. Conan, R.W. Elner, W.D. McKone, and D.M. Taylor

Summaries of each of the presentations made at the workshop are given below, along with comments made by participants. The complete texts for most presentations are given in following sections in this volume.

I. Stock Definition and Larval Mixing

The literature on stock definition and larval mixing for the snow crab, *Chionoecetes opilio*, was reviewed. A study of morphometric, meristic, electrophoretic and fecundity comparisons for snow crab from Atlantic Canada indicated that there are at least four phenotypic stocks and three genetic stocks. However, the study did not consider potential bias due to variations in the proportion in terminal moult males in the samples. As there can be differences in responses to exploitation in management areas within any one genetic stock, a phenotypically and/or genetically defined stock might be subdivided into more practical units that reflect intra-stock factors such as growth and recruitment patterns. There is some evidence of self-sustaining populations within the Gulf of St. Lawrence. Given known larval mixing characteristics each stock probably covers a large geographical area, with the precise boundaries between stocks fluctuating. This needs more investigation.

C. opilio has a reported larval phase of between 66 days to 7-8 months although 3-4 months appears to be most accepted. Surveys in the Japan Sea, southwestern Bering Sea, and the Gulf of St. Lawrence have shown substantially different depth distribution patterns for snow crab larvae. The vertical distribution of larvae can profoundly influence their development time and eventual settling position. Considering recruitment mechanisms for decapod larvae in general, it appears unlikely that *C. opilio* should be considered as a passive drifter in surface currents. However, mechanisms that might influence snow crab larval dispersal have not been evaluated. Some larvae are probably dispersed over a wide area. Consequently, given adult male snow crabs do not generally show either clear or extensive patterns of movement, it is probable that stocks will be large and 'plastic'. In addition, high inter-annual variability in larval abundance (due variously to egg production, larval survival and transport patterns) can be expected to be the cause of sporadic recruitment, a phenomenon characteristic of many crab fisheries.

Comments - Suggestion that electrophoresis should also be carried out on larvae as well as adults in order to better determine stock mixing patterns.

- There was dicussion about system continuity, with evidence for larval retention as well as larval dispersal.

- Although there is a fairly large amount of information on snow crab larvae along the Scotian Shelf, it was cautioned that such larvae are over a marginal snow crab habitat and could represent a leakage from the major system upstream.
- There was discussion on the diet of *Chionoecetes* larvae. Alaskan studies on *C. bairdi* and king crab emphasized the importance of diatoms in diet and synchronization of larvae to algal blooms ("match-mismatch" hypothesis).
- Discussion emphasized two aspects of larval biology, which are not mutually exclusive: 1) factors influencing larval transport and their impact on stock boundaries; 2) factors influencing larval survival and hence recruitment success.
- There was a suggestion that the physical and biological characteristics of water masses in terms of potential for growth and survival of larvae be tested through bioassay techniques, as is being done for king crab in Alaska.

II. Growth of Snow Crab

Presentation

Moulting is a cyclic phenomenon through which crab shed their old shells and grow. Timing of both moult and reproduction is tuned to environmental factors. For Gulf of St. Lawrence snow crabs, ecdysis generally occurs in the spring. Moult frequency may vary with size with older animals tending to moult less frequently, i.e., with longer intermoult periods. There are spatial variations in the timing of moult. Growth models must consider growth increment as well as periodicity. Majidae is a crab family characterized by a terminal moult to morphometric maturity, which can occur through a wide size range.

Various models to describe growth increment in snow crab were discussed. The allometric relationship between claw size and body size in males was evaluated. This relationship allows identification of morphometrically immature (i.e., preterminal moult) individuals. Intermoult staging in snow crab can be readily determined by the examination of mouth parts and histology of the exoskeleton.

Comments - Discussion focussed around defining maturity in both males and females. The following was accepted:

1. In female *C. opilio*, the ovary begins to mature in the pre-puberty stage and there is a moult at which time the abdomen and pleopods undergo substantial changes. This is commonly referred to as the 'puberty' or 'maturity' moult. Females do not moult after this terminal moult, and

only copulate and lay eggs after this moult. Repeat copulations may occur over a number of years.

2. a) Male C. opilio have a moult which is discriminated by a change in the allometric relationship between claw and carapace sizes. This moult is homologous to the 'puberty' moult described in many other majids. In east coast C. opilio there is considered to be no moulting after this moult. The most likely assumption is that this also applies to other Chionoecetes species and populations.

b) A recent thesis indicated all males have begun spermatogenesis at a CW of 40 mm, before the 'terminal (puberty)' moult. This may be several instars prior to the terminal moult.

c) The data concerning whether or not preterminal males can effectively reproduce in the field are equivocable. There is controversy as to whether all mating males in the field are terminal or not. There is uncertainty as to whether laboratory observations apply to the field. There are confirmed reports of mating by preterminal C. bairdi males with primiparous females, with subsequent moulting of the males.

d) There is controversy as to the relative contribution of terminal males (95mm) in successfully mating with multiparous females in the field.

- It was stressed that aquarium experiments must be viewed with caution because they are made under stressful conditions that may result in abnormal behaviour.

- An hypothesis was put forward that size at terminal moult could be related to density-dependent factors such as the prevalence of larger mature animals. Animals must optimize their probability of survival against that of successfully mating. Mating success is maximized at a large size, while a terminal moult at a smaller size may reduce the risk of mortality before contributing to reproduction.

- Maturity is a complex phenomenon involving behaviour, morphology, physiology and ecology, and may be affected by the presence of a fishery.

- The Y-organ, responsible for the secretion of a moulting hormone, has been histologically observed to degenerate in mature animals of both sexes. However, in contrast to what was reported for one other majid species, it was never totally absent in C. opilio. This implies that this gland may have additional role(s) in snow crab physiology.

- It was indicated that information on growth of prerecruits, pertinent to stock-recruitment relationships, was available in a thesis.

III. Maturity and Mating Relative to Stock Management

Presentation

The presence of spermatophores in the vas deferens is not necessarily an indicator of sexual maturity in C. opilio, but it may be in C. bairdi. Morphometric and functional maturity information was discussed. There was debate, based on both field and laboratory information, over whether terminal males < 95 mm CW are likely to contribute to any significant extent in mating with multiparous females, i.e., females in a hard shell state in their terminal moult.

While it is uncertain what type of males (preterminal or terminal) can mate with primiparous females, successful reproduction may decrease with heavy exploitation of males > 95 mm CW. Furthermore, it was stressed that all males are unable to successfully mate until their shells are sufficiently hard.

The literature on maturity in females and the relative contribution of primiparous and multiparous females to population fecundity was reviewed. While primiparous mating probably occurs in February, multiparous mating is delayed until after egg-hatching in May-June.

Comments - Considerable discussion revolved around whether a stable population fecundity was being maintained under the present fishing regime.

- In eastern Canada, the incidence of egg-bearing females appears close to 100%. However, some caution was advised in interpreting these data due to the ability of females to retain unfertilized egg masses and the possibilities for later egg loss due to causes such as parasitism and predation during brooding. Nevertheless, there appeared a general consensus that population fecundity was currently high and changes in yield were not likely due to decreased population fecundity. It was pointed out that the major Gulf fishery is relatively recent in relation to the presumed life-span (at least 5-10 years) of the species and that there had probably not been time for the fishery to impact on stock fecundity.
- There was discussion on observations of mating in Bonne Bay, Newfoundland. For instance, no primiparous female has been observed to mate, but it should be noted that the absolute abundance of these females was apparently particularly low at the time of observations, i.e. in recent years.
- It was noted that although the fishery (males only) increased in the early 1980's and has recently declined in the southwestern Gulf, the proportion of females bearing eggs is unaffected.

- There was discussion of the fact that in C. bairdi, primiparous females only produce approximately 70% of the eggs of multiparous females

- It was suggested that the proportion of terminal males under 95 mm CW in the catch had increased since the beginning of the fishery.

- It was cautioned that the presence of eggs does not necessarily translate into successful larval production. Also, a real reduction in population fecundity could still occur. As it is, the present drop in catches may be due to the removal of a standing stock of large males in terminal moult and does not appear due to past population fecundity reduction.

- For future research, it was suggested that egg viability be ascertained through histology or evidence of developmental activity. It was proposed that there should be an experimental fishery in which males were fished heavily at a small size to test stock reactions.

- There was some contention over whether or not the Gulf fishery is still experiencing a fishing down of accumulated terminal males or whether this occurred in the 1970s. In support of the latter, it was mentioned that the Gulf fishery had been closed in the 70's due to the high incidence of soft shelled crabs. It was reiterated that although there is no evidence for a reduction in population fecundity at the present time, the future is less certain.

- Recent recruitment may not be sufficient to maintain catch rates at earlier fishery levels.

IV. Reproductive Biology

Presentation

Information relative to population fecundity in snow crab was reviewed. This included size-fecundity relationships for both primiparous and multiparous females and the phenomenon of egg-loss during the brooding period. Additional information was presented on reproductive alternatives (use of fresh vs. stored sperm) and latitudinal gradients in fecundity. There was evidence for considerable egg loss during the brooding period due to causes such as loss of unfertilized eggs, predation, parasitism, and physical loss.

Comments - Unpublished information was presented on mating success in C. bairdi. It appears that males >100 mm CW are more likely to successfully mate with both primiparous and multiparous females.

- Some discussion focussed on the life-expectancy of multiparous females. Reference was made to a female senescence that occurred off eastern Cape Breton when there had been no recruitment for several years.

- There was debate regarding the ability of preterminal males to mate arising from experiments conducted in the Gulf and Newfoundland regions.

- Evidence was debated on the characteristics for distinguishing old from freshly deposited sperm. It was pointed out that the presence of fresh grasping marks on the female's shell could serve as corroborating evidence for recent pairing.

- While the consensus was that small males could perhaps mate with multiparous females, it was agreed that they were not as successful as large males when placed in competition with them or when placed with larger females.

- Finally, statements were made that in C. bairdi, it is the small males that mate with primiparous females and large males with multiparous females.

V. Distribution and Movement

Presentation

Snow crab live most commonly on mud or sand-mud bottoms in temperatures ranging from -0.5 to 5.0°C. Mature females and immatures were highly aggregated, whereas large males approached a random distribution in an early photographic study. Immature juveniles are often seen on mud-gravel substrates in shallower waters. There is evidence that they migrate to deeper muddy bottoms as they reach maturity. Smaller juveniles are often observed on the same muddy bottoms as the adults.

A statistical analysis of population size distribution supports the hypothesis of two waves of annual recruitment to the fishing grounds, one composed of crabs moulting to legal size on the fishing grounds and the other composed of crabs migrating to the fishing grounds later in the season.

a) Local movements: Activity appears to be related to light level, with crabs more active in the dark.

b) Large-scale movements: Several tagging studies report that, in eastern Canada, the majority of >95 mm crabs move less than 25 km between tagging and recapture. More thorough analysis of movement in the context of time at large and tagging location is required. These movements appear undirected. However, some observations such as the breeding migration studies in Bonne Bay suggest directed seasonal migrations.

Apart from dispersal during the larval period, extensive mixing between distinct groups of crabs in Atlantic Canada is not likely to occur to any great extent.

Comments - It was suggested that the distributional patterns of groups could be explained by social/ecological interactions such as the exclusion of smaller crabs by larger crabs.

- There was a discussion about whether ecological factors such as the presence of shelter and appropriate food sources could explain the presence of smaller juveniles on heterogenous bottoms and larger crabs on muddy substrates.

- It was suggested that ultrasonic telemetry is one of the most appropriate tools for studying small-scale movement, although it is a rather expensive technique.

- It was suggested that the scale of substrate patchiness which could be studied though bottom photography (still or video) or side-scan sonar, has a direct impact on the interpretation of small-scale distribution and movement of all sizes of crabs.

- Conventional tagging has a serious limitation as it only provides information about net movement between tagging date and recapture date.

- It was explained that, in the past, most tagging studies were designed for stock size evaluation rather than for movement studies.

- It was mentioned that the limited movements of crabs during the fishing seasons in relation to spatial and temporal exploitation patterns of the fleet can cause bias in the results of the Leslie analysis.

VI. Natural Mortality

Crab species are subjected to many different sources of mortality during the various phases of their life-history. During the egg stage they are vulnerable to mechanical abrasion, parasites and diseases. Mortality is probably most variable at the larval stage. Larval survival may depend on variable oceanographic conditions, appropriate food sources, limited predation and suitable settlement conditions.

Juvenile and adult crabs are preyed on by numerous species (as many as 14 in Alaska). In eastern Canada, cod and skate are identified as major predators. Limited cannibalism does occur. Quantity of crab consumed by predators has been estimated for some areas over a limited time period, but does vary according to numerous ecological factors. The incidence of predation also has a strong seasonal component.

Crabs can be host to several symbiotic organisms including fungi, bacteria, bryzoans, hydroids, polychaetes, leeches and barnacles. Their impact on annual mortality is probably negligible. There are also sources of indirect fishing mortality such as gillnetting, trawling, trap ghost fishing, and trauma due to rough handling of small crabs by fishermen.

Comments - Current estimates of natural mortality for snow crab in eastern Canada are arbitrary.

- The mortality rate probably varies between life-cycle stages but one should be concerned that variation could be important within a single stage, between individuals, and between different groups of individuals, depending upon the environmental conditions they face.
- It was pointed out that juvenile survival is probably limited by the number of suitable sites available, which may act as a bottleneck to recruitment.
- Research on egg mortality, particularly by predators, is desirable.

VII. Modelling

A model, based on simple *a priori* assumptions, describing the distribution of crabs in moult classes was presented. When natural mortality decreased as a function of size, the effects of fishing were quite pronounced. A virgin stock is composed of larger animals with a low moulting percentage. Fishing animals of legal size reduced the standing stock of large animals by more than a factor of 10 and increased the moulting fraction.

Yield estimates were presented from an equilibrium model which excluded smaller animals from successful mating. Also, yield estimates were produced when only terminal animals were reproductive. The modelled stock was seen to be very sensitive to exploitation if only large terminal males were reproductive. The yield cycles in dynamic simulations became damped out when only terminal males were reproductive.

Model results suggested that the current high exploitation, 60-80%, in both the Atlantic and Bering Sea fisheries was not consistent with only large, terminal males being reproductive.

Comments - It was pointed out that the model showed that suitable reproductive potential does not guarantee suitable recruitment to the fishery.

- It was argued that, given the abundance of terminal moult crabs in the fishery, one does not have to use sophisticated models to predict the best yield-per-recruit with high exploitation rates. To maximize yield, there is no point in leaving animals that have stopped growing on the bottom, except perhaps for reproductive purposes.

- A discussion ensued on the available information on snow crab growth that is useful for such models. The question was raised that little was known about moult intervals. Nevertheless, it was mentioned that the frequency of moult in a given size distribution is a convenient way of approaching the problem.

- There was a debate about the relevance of developing such models in the absence of substantial detailed information but proponents argued that the models helped identify the most sensitive variables.

VIII. A) Growth and moulting

a) Does male growth continue after sexual maturity?

Four types of information supporting the argument that males continue to moult after sexual maturity were discussed:

1. The literature states that in larger size males, there seems to be a decrease in the frequency of moulting and that there are one or two moults after maturity.

2. From unpublished data (1974-1987) from the Bering Sea, there seemed to be annual moulting of 80%-90% of males, with two exceptions, 1980 and 1982. For larger size animals in these years, moulting appeared to be delayed until the next year.

3. Analogies to other co-generics: In _C. bairdi_, males have been observed in the laboratory to mate and subsequently moult. Furthermore, 87% of mature females (which all agree have a terminal moult) sampled have barnacles, whereas none of the 2,000 males observed in the study had barnacles.

4. Bacterial lesions on the shell were observed in _C. tanneri_ females but not in males, despite the fact this species is not commercially exploited. This suggests that male _C. tanneri_ may have no terminal moult after maturity.

In the Bering Sea, there exist areas where there are large numbers of old-shelled males.

b) Is there a terminal moult and variable size at sexual maturity?

Information was presented that _C. opilio_ males do not continue to moult after maturity. Most studies that suggest they do were based on tentative observations in an early Japanese paper, and fisheries biologists have since used a single cut-off point to define maturity. This method may have been effective in pre-fishery populations where there was a clear size separation between mature and immature individuals. However, with the imposition of a fishery, relative abundance at morphometric stage has changed and currently preterminal and terminal males overlap in size.

A terminal moult can occur over a large range of sizes and, perhaps, ages. Scientific data was presented that separated terminal males, preterminal males with mature gonads, and juveniles. Studies to compare the size distributions of these groups of males were advocated.

It was stated that the Y-organ is responsible for a pre-moulting hormone and an ecdysis factor. All the literature on majiids reports that a puberty moult is the terminal moult, and this moult is followed by Y-organ atrophy or loss.

It was also stated that at the very least, there was a transformation, if not degeneration, of the Y-organ following terminal moult. Definite conclusions have yet to be drawn and await completion of an on-going study.

Discussion: There was consensus that male snow crabs in the Gulf of St. Lawrence exhibit a terminal pubertal moult. This is in accordance with all observations on a wide variety of other majid species. The burden of proof in other areas is now to show that terminal moult does not exist. The evidence presented for the Bering Sea, while not conclusive, suggested that male Chionoecetes opilio continue to moult throughout their size range and that the reproductive potential of the stock is being maintained. Additional morphometric and histological information is required to ascertain whether there is a terminal moult at puberty there.

However, for male C. bairdi, the terminal moult is not necessarily the puberty period. Significant numbers of males moult after successful mating. This point is still unresolved for C. opilio in the Pacific.

Observations in the Bering Sea for C. opilio are consistent with a terminal moult if animals are being consistently removed from the sea after terminal moult.

B) Variables affecting recruitment

i. Reviewed evidence for and against the null hypothesis that the fishery has had no impact on the level of recruitment to the commercial fishery.

ii. Reviewed evidence for and against the null hypothesis that density-dependent factors have no impact on the level of annual recruitment to the commercial snow crab fishery.

iii. Reviewed the potential influences of density-independent factors on recruitment.

iv. Presented an hypothesis, based on physiological measurements in the laboratory, that both growth and reproduction can be critically limited by temperature, and that there may be an advantage to crabs moving in response to ambient water temperature.

Discussion

There was a suggestion that the occurrence of juveniles in shallow water may be a temperature-related phenomenon. It was suggested that movement in response to water temperature would have to be field tested by electronic tagging. It was noted that females tagged after mating in Bonne Bay and the Japan Sea move inshore to shallower, warmer water; such behaviour could influence egg development rates. A general comment was that more physiological studies are required and that such work might explain some ecological observations. It was pointed out that most snow crabs in eastern Newfoundland have no opportunity to change their temperature requirements by moving to deeper water as they are at the maximum water depth already.

This latter point was used as an argument to reinforce the hypothesis for growth and recruitment into the Newfoundland fishery being temperature controlled. Unpublished laboratory observations showed females hatching their eggs at -2°C to 2°C and subsequent larval development. Published laboratory observations show snow crabs moulting at 0°C-1°C. It was cautioned, however, that one should consider the accumulated degree days in such observations.

Arguments were made that the collapse of the east Cape Breton snow crab stocks should not be interpreted as a fishery-caused phenomenon. The collapse may have resulted from lack of larval dispersal to the area and marginal habitat.

Questions were asked regarding abundance of juvenile snow crab. It was stated that in Bonne Bay there is a new influx of prerecruits. Similar statements were made for eastern Cape Breton snow crab, Bering Sea king crab, and Dungeness crab. Recruitment is considered sporadic in many crab fisheries.

Two testable hypotheses were proposed:

1) Removal of large terminal males causes increased growth rate and/or recruitment of small males to the fishery.

2) Removal of large males has an impact on population fecundity. This is testable by observing egg fertilization proportion and incidence of ovigerous females.

With regards to (2) above, it was indicated that at the low temperature on snow crab grounds, unpublished data indicated that egg decay rates are low and non-fertilized eggs could persist for up to eleven weeks.

Discussions focused on the uncertain relationship between population fecundity level, larval abundance and subsequent recruitment. While it has been observed in other species that strong year-classes may come from relatively low population fecundity levels, we should be concerned that the C. opilio fishery might be concentrated on a single year-class. Therefore, the potential exists for negatively influencing population fecundity at present catch rates.

A counter argument was presented in that females might benefit from a fishing of males by having additional food and space. There was debate on whether trap catch rates accurately reflect abundance patterns and recruitment strength. Trap data can provide useful indices of abundance, but additional factors such as temporal fishing pattern and precise and accurate fishing location reporting need to be considered.

There was reiteration of the arguments that fishing intensity in the Gulf of St. Lawrence had only been high for the past five years. Hence, it is premature to expect that adverse influences on population fecundity should be apparent at this time. Certainly, there now appears to be good evidence that population fecundity is not necessarily fully protected by the 95mm size limit. While this observation does not necessarily mean there is a problem, it does indicate we should be cautious.

It was recommended that female fecundity be regularly monitored and that monitoring should include examination of spermatheca and gonadal condition.

Evidence suggests that there have been changes in growth and/or survival as a result of fishing, e.g. in the virgin situation, terminal moult males may have repressed the growth of preterminal moult males or decreased their survival. It appears that preterminal moult males are relatively more abundant now than in the pre-fishery situation.

There was considerable discussion on catch rate and production trends and the potential impact of the fishery on these. It was again pointed out that there was no evidence that the fishery had influenced recruitment to date.

Possible mechanisms causing males to mature at smaller sizes and for causing a reduction in the relative numbers of large males were discussed. There was general concurrence that there was insufficient evidence to reject the null hypothesis that the fishery has had no impact on recruitment to the grounds.

Yield and historical fishing patterns in the Gulf of St. Lawrence were discussed. There was debate on whether or not the present situation represents the continued fishing out of a virgin stock or whether the virgin stock was fished out in the 1970's. However, it was agreed that precise and accurate fishing location data is essential in future studies. Furthermore, it was proposed that experimental fishing is perhaps the only method by which to resolve questions as to the impact of the fishery upon recruitment levels.

It was agreed that size frequency and shell condition data alone are useful only for certain purposes. However, future workers should supplement such data with information on moult stages, morphometrics, egg viability, at sea catch sampling and precise fishing locations.

Arguments again revolved around the "preoccupation" with population fecundity levels in snow crab. There was sharp disagreement on whether or not this was indeed a real problem.

There was debate on the relationship between the spring phytoplankton bloom and larval survival. Similarly, attention was focussed on the survival of other life-history stages. It was agreed that a "critical life-history stage" probably varies from year-to-year and thus prediction of recruitment is necessarily a complex operation. Nevertheless, workers should investigate prerecruit abundance of juveniles by trawling and should also further investigate factors influencing larval survival and dispersal.

In conclusion, there appeared to be insufficient evidence to either accept or reject the null hypotheses on density dependent and density independent effects. Debate identified critical gaps in the knowledge necessary to resolve these issues.

IX. Summary of Exploitation History

The snow crab fishery in Atlantic Canada has developed over the last twenty years. Stock status and fishing activities are monitored through the analysis of commercial catch statistics, including sales slips and logbooks, and through the analysis of research activities in estimating abundance and other biological parameters. Initial regulations were based only on processing considerations. The use of trawl gear was forbidden to minimize habitat destruction and damage to crabs. Females were excluded from the catch due to their small size; only large males, >100 mm CW, were considered exploitable. Subsequently, the size limit was reduced to 95 mm CW when the industry became capable of processing smaller crabs.

In the mid-1970's, effort restrictions were introduced by limiting access to the fishery, as well as limiting the number of traps. As catches increased, management established zones, and a limited number of local fishermen were granted exclusive access. In the inshore fisheries, it was envisioned that fishermen would not receive all their income from crabs, but would also be involved in other fisheries. In a few zones, a preemptive total allowable catch (TAC) was established and each boat was given an individual quota. TACs were initially based on the estimated average annual biomass increase (Cape Breton), 50-60% of the exploitable proportion of the resource (Newfoundland), and finally on historical trends of harvest (southwest Gulf).

With increasing exploitation, the relative proportion of soft-shell crabs increased due to fishing in the moulting time period. To overcome this problem, regulations were introduced to limit the fishing season by a summer closure. To overcome problems in catching undersized crabs, a minimum trap mesh size regulation was introduced.

Ideally, managers would like to obtain precise estimates on stock size from CAFSAC for each individual stock. They would like to know when moulting will occur, have clearly defined stock boundaries, and know what maximum annual catch should be permitted, without threatening the continuity of the fishery.

This information is not available for all stocks, consequently discussions on TAC's become difficult on some occasions and controversies are sometimes difficult to settle. CAFSAC is often required to provide advice generated on arbitrary assumptions. A "guess-timate" has been regarded as more useful than no estimate at all.

X. Implication of Biology on Management

The biological data presented was summarized in the context of management and its perceived relevance and deficiencies in terms of future exploitation options. It was stated that landings from different management areas have either declined, increased or remained stable. It was difficult to assess if an overall regional pattern exists. General observations were that recent fisheries have tended to exceed recommended exploitation rates. In some cases, this may have caused a general decline in abundance. There is also an increase in the soft-shell problem and in the occurrence of sublegal size crabs in catches. The reproductive capacity of the population may not be protected by current regulations, given the above. With the relative reduction in abundance of larger crabs, the existing annual fishery is now largely harvesting only each year's recruitment, and the buffering capacity to sustain comparable annual landings may be reduced. Future landings will depend largely on the level of that year's recruitment to the fishery.

The implications for management of our current understanding of snow crab biology are that with better knowledge of growth, target fishing mortality by size class may change and that a reduction in landings may be recommended. Associated with this, pulse fishing of grounds and rotation of fishing between alternate grounds may be desirable as a mechanism to both decrease fishing mortality and to build up a large number of exploitable age size classes. Allowing fishermen to exploit smaller terminal moult crabs in a pulse fishery may be desirable. This might be achieved with a minimum claw size limit rather than minimum carapace width limit. It is not presently clear why female reproduction should be maintained at 100%, since no stock recruitment relationship has been established and crab are unique in that females are unexploited. It remains to be established if recruitment overfishing is really a concern. Relative movement of crab versus the fishing fleet may compromise use of the Leslie model in stock assessments. Refinement of natural mortality estimates by size may also influence targeted size class, since it is accumulative with fishing mortality.

Suggested research priorities by topic are:

1) Growth - data needs to be summarized and growth patterns and rates better documented. Establishing estimated ages of recruitment to the terminal moult cohort is needed for population modelling and establishment of the potential for growth overfishing.

2) A functional fishery-independent method of establishing prerecruit male abundance is needed.

3) The quality of catch and effort data needs improvement, both in terms of completeness and in the nature of the data collected. This may not be as important for within-year comparisons as for between-year comparisons, and is required to establish trends in population abundance related to evaluating the impact of the fishery on the resource.

4) The role of <95 mm CW, terminal moult males in reproduction should be resolved because of the general reduction in abundance of larger males and possible future recruitment overfishing.

Comments: It appears, from the limited data presented, that fishing may have a positive effect on juvenile abundance. If so, then we need:

a) growth and natural mortality rates for males >70 mm CW;

b) the percentage moulting to the terminal instar in each size class.

Having this data would allow determination of yield per recruit recommendations for crab >70 mm CW for different fishing mortalities and minimum size limits.

I. RAPPORT DE L'ATELIER

par

G.S. Jamieson, R. Bailey, G.Y. Conan, R.W. Elner, W.D. McKone, et D.M. Taylor

Ci-après vous trouverez les sommaires de chaqune des présentations faites lors de l'atelier, ainsi que les commentaires des participants. Les textes complets pour la plupart des présentations sont présentés dans des sections de ce volume.

I. Délimitation des stocks et mélange des larves

On a examiné les données publiées sur la délimitation des stocks et le mélange des larves dans le cas du crabe des neiges *Chionoecetes opilio*. Une comparaison des caractères morphométriques, méristiques et électrophorétiques ainsi que des taux de fécondité du crabe des neiges de l'Atlantique canadien a révélé l'existence d'au moins quatre stocks phénotypiques et trois stocks génétiques. Toutefois, cette étude n'a pas tenu compte du biais potentiel entraîné par les variations du nombre relatif de mâles en phase terminale dans les échantillons. Étant donné qu'il peut y avoir au sein de chaque stock génétique des différences de réaction à l'exploitation dans chaque secteur de gestion, un stock phénotypique ou génotypique peut être sous-divisé en unités plus pratiques qui traduisent des facteurs intra-stocks comme les régimes de croissance et de recrutement. Certaines données portent à croire à l'existence de populations indépendantes dans le golfe du Saint-Laurent. Étant donné les caractéristiques connues du mélange des larves, chaque stock fréquente probablement une grande superficie géographique où les limites précises entre les aires de répartition des stocks fluctuent. Ceci requiert des études plus poussées.

Chez *C. opilio*, la phase larvaire dure de 66 jours à 7-8 mois quoique 3-4 mois semblent être la norme. Les résultats de relevés effectués dans la mer du Japon, le sud-ouest de la mer de Béring et le golfe du Saint-Laurent ont révélé que les larves du crabe des neiges connaissent des régimes de répartition selon la profondeur nettement différents. La répartition verticale des larves peut profondément influer sur la durée du développement et l'emplacement du site éventuel de colonisation. Si l'on tient compte des mécanismes de recrutement des larves de Décapodes, il semble peu probable que *C. opilio* devrait être considéré comme un organisme passif qui dérive au gré des courants de surface. Toutefois, on n'a pas évalué les mécanismes qui peuvent influer sur la dispersion des larves du crabe des neiges. Il est probable qu'un certain nombre de larves sont dispersées sur une grande superficie. Par conséquent, vu que les mâles adultes ne manifestent généralement pas des régimes de migration précis ou importants, il est probable que les stocks sont importants et "souples". De plus, on doit s'attendre à ce que la variabilité inter-annuelle élevée de l'abondance des larves (entraînée variablement par la production d'oeufs, la survie des larves et les régimes de transport) soit la cause d'un recrutement irrégulier, caractéristique de nombreuses pêcheries du crabe.

Commentaires - On propose la réalisation d'études électrophorétiques de larves et d'adultes afin de mieux déterminer les régimes de mélange des stocks.

- On délibère de la question de la permanence du système en fonction de données sur la rétention et la dispersion des larves.
- Quoiqu'on dispose d'un assez grand nombre de données sur les larves du crabe des neiges de la plate-forme Scotian, ces larves fréquentent un habitat marginal et peuvent représenter une fuite de l'important système situé en amont.
- On discute de la question du régime des larves de Chionoecetes. Des études menées en Alaska sur C. bairdi et le crabe royal ont mis l'accent sur l'importance des diatomées dans le régime alimentaire et la synchronisation de la présence des larves et des efflorescences phytoplanctoniques (hypothèse du "match-mismatch").
- On met l'accent sur deux aspects de la biologie des larves qui ne sont pas mutuellement exclusifs : 1) les facteurs qui influent sur le transport des larves et leurs incidences sur les limites des stocks; 2) les facteurs qui influent sur la survie des larves et donc sur le succès du recrutement.
- On propose que les caractéristiques physiques et biologiques des masses aqueuses au point de vue du potentiel de croissance et de survie des larves fassent l'objet d'analyses biologiques comme dans le cas du crabe royal en Alaska.

II. Croissance du crabe des neiges

Sommaire

La mue est un phénomène cyclique qui permet au crabe des neiges d'augmenter de taille chaque fois qu'il rejette sa vieille carapace. Le moment de la mue et de la reproduction est synchronisé à des facteurs environnementaux. Dans le cas du crabe des neiges du golfe du Saint-Laurent, l'exuviation a généralement lieu au printemps. La fréquence des mues peut varier selon la taille; ainsi, les vieux crabes ont tendance à muer moins fréquemment c.-à-d. que les périodes d'intermue sont plus longues. Il existe des variations spatiales du moment de la mue. Les modèles de croissance doivent tenir compte des incréments de croissance ainsi que de la fréquence. des mues. Chez les Majidés, la mue terminale coïncide avec la maturité morphométrique qui peut avoir lieu à un grand écart de taille.

On étudie divers modèles de description des incréments de croissance chez le crabe des neiges. La relation allométrique qui existe entre la taille du chélipède et la taille du corps des mâles permet l'identification des individus immatures au niveau morphométrique (c.-à-d. en phase de mue préterminale). On peut facilement déterminer la période d'intermue par l'examen des parties buccales et l'étude histologique de l'exosquelette.

Commentaires - Au cours de la discussion centrée sur la définition de la maturité chez les mâles et les femelles, on a accepté les points suivants (1, 2 d) :

1. Chez la femelle de C. opilio, la maturation de l'ovaire commence à la prépuberté au moment de la mue communément appelée "mue de puberté" ou "mue de maturité" où l'abdomen et les pléopodes subissent d'importantes modifications. Celle-ci représente la dernière mue chez la femelle dont les rôles se limitent, à partir de ce moment, à l'accouplement et à la ponte. L'accouplement répété peut avoir lieu pendant un certain nombre d'années.

2. a) On observe chez le mâle de C. opilio une mue caractérisée par une modification de la relation allométrique entre la taille du pléopode et la largeur de la carapace. Cette mue correspond à la "mue de puberté" décrite chez de nombreux autres Majidés. Chez C. opilio de la côte est, on croit qu'elle représente la dernière mue. Il est fort probable que ceci s'applique aussi d'autres espèces et populations.

   b) Selon des données récentes présentées dans une thèse, la spermatogénèse commence chez tous les mâles dont la carapace a atteint une largeur de 40 mm, soit avant la mue "terminale (de puberté)". Ceci peut représenter plusieurs stades larvaires avant la mue terminale.

   c) Les données visant à déterminer si les mâles en phase préterminale peuvent en réalité s'accoupler ou non sont ambiguës. Les opinions sont partagées quant à savoir si tous les mâles géniteurs en milieu naturel sont en phase terminale ou non. Il existe un certain doute quant à l'application des observations expérimentales à la situation en milieu naturel. Il existe des observations confirmées d'un accouplement de mâles de C. bairdi en phase préterminale avec des femelles primipares suivi d'une mue des mâles.

   d) La contribution relative de mâles en phase terminale (<95 mm) à l'accouplement fructueux avec des femelles multipares dans le milieu naturel est sujet à débat.

   - On souligne que les résultats d'expérience en aquarium doivent être considérés avec circonspection étant donné qu'ils sont recueillis dans des conditions de stress qui peuvent amener un comportement anormal.

   - On avance l'hypothèse que la taille au moment de la mue terminale peut être en relation avec des facteurs liés à la densité comme le nombre de gros animaux matures. Les crabes doivent optimiser leur probabilité de survie compte tenu de la nécessité de s'accoupler avec succès. Le succès de l'accouplement est maximisé à une grande taille tandis qu'une mue terminale à une petite taille peut réduire le risque de mortalité avant que l'individu puisse s'accoupler.

- La maturité est un phénomène complexe où interviennent le comportement, les caractères morphométriques, la physiologie et l'écologie; l'exploitation peut influer sur ce phénomène.
- Des études histologiques ont révélé que l'organe Y responsable de la sécrétion d'une hormone d'exuviation subit une dégénérescence chez les animaux matures des deux sexes. Toutefois, cet organe n'est jamais complètement absent chez C. opilio contrairement aux observations signalées pour une autre importante espèce de Majidés. Ceci signifie que cet organe peut jouer d'autres rôles dans la physiologie du crabe des neiges.
- On note que des données sur la croissance des prérecrues pertinentes aux relations stock-recrutement sont présentées dans une thèse.

III. Maturité et accouplement par rapport à la gestion des stocks

Sommaire

La présence de spermatophores dans le canal déférent ne constitue pas forcément un indicateur de la maturité sexuelle chez C. opilio mais ceci peut être le cas chez C. bairdi. On étudie les données sur les caractères morphométriques et la maturité fonctionnelle. D'après des données recueillies sur le terrain et en laboratoire, on tente de déterminer si les mâles en phase terminale de <95 mm LC sont susceptibles de contribuer de façon importante à l'accouplement avec des femelles multipares, c.-à-d. des femelles à carapace dure en phase terminale.

Quoiqu'il soit incertain quel genre de mâles (en phase préterminale ou terminale) peut s'accoupler avec des femelles primipares, ces observations portent à croire que le succès de l'accouplement peut diminuer à cause d'une forte exploitation des mâles de >95 mm LC. De plus, on souligne que tous les mâles ne peuvent s'accoupler fructueusement qu'après le durcissement suffisant de leur carapace.

On examine les données publiées sur la maturité chez la femelle et la contribution relative des femelles primipares et multipares à la fécondité d'une population. L'accouplement des femelles primipares a probablement lieu en février mais l'accouplement des femelles multipares n'a lieu qu'après l'éclosion des oeufs en mai ou juin.

Commentaires - Le maintien d'un taux de fécondité stable étant donné le régime actuel de pêche a été longuement débattu.

- Dans l'est du Canada, la fréquence de femelles oeuvées semble s'approcher de 100 %. Toutefois, on recommande une certaine prudence dans l'interprétation de ces données étant donné la capacité des femelles de garder des oeufs non fertilisés et la perte potentielle subséquente des oeufs entraînée par le parasitisme et la prédation pendant l'incubation. Malgré tout, on semble être d'accord que le taux de fécondité est actuellement élevé et que les variations du rendement ne sont pas le résultat d'un taux de fécondité diminué. On souligne que la principale exploitation dans le golfe est relativement récente par rapport à la durée de vie supposée de l'espèce (au moins de 5 à 10 ans) et que la pêche n'a probablement pas encore influé sur le taux de fécondité du stock.

- On examine les observations recueillies sur l'accouplement du crabe dans la Bonne-Baie (Terre-Neuve). Par exemple, l'accouplement de femelles primipares n'a pas été observé mais on doit noter que l'abondance absolue de ces femelles était en apparence particulièrement faible au moment de l'étude, c.-à-d. au cours des dernières années.

- On note que malgré l'intensification de la pêche (des mâles seulement) au début des années 1980 et son déclin récent dans le sud-ouest du golfe, le nombre relatif de femelles oeuvées demeure le même.

- On traite du fait que chez C. bairdi, la production d'oeufs chez les femelles primipares n'atteint qu'environ 70 % de celle observée chez les multipares.

- On avance l'hypothèse que le nombre relatif de mâles en phase terminale dont la largeur de la carapace est inférieure à 95 mm présents dans les prises a augmenté depuis l'ouverture de la pêche.

- On doit noter que la présence d'oeufs ne signifie pas forcément une production fructueuse de larves. De plus, une diminution réelle du taux de fécondité pourrait néanmoins avoir lieu. Dans la situation actuelle, la baisse des prises peut être le résultat de la disparition d'un stock actuel de gros mâles en phase terminale et ne semble pas être liée à une baisse passée du taux de fécondité.

- Pour ce qui est des activités de recherches futures, on mentionne la détermination du taux de viabilité des oeufs grâce à des études histologiques ou des données sur le développement. Afin de déterminer les réactions du stock, on devrait effectuer une pêche expérimentale qui amènerait une forte exploitation des mâles de petite taille.

- On ne sait pas vraiment si la pêche dans le golfe porte toujours sur la biomasse accumulée de mâles en phase terminale ou si cela s'est produit pendant les années 1970. À l'appui de ce dernier point, on note que la pêche dans le golfe avait été fermée pendant les années 1970 à cause de l'incidence élevée de crabes à carapace molle. On répète que l'avenir est moins certain même si rien n'indique une baisse du taux de fécondité actuel.

- Il est possible que le recrutement récent ne suffise pas à maintenir les taux de capture au niveau antérieur.

IV. Reproduction

Sommaire

On étudie les données sur le taux de fécondité du crabe des neiges, notamment les relations taille-taux de fécondité chez les femelles primipares et multipares et la perte d'oeufs pendant l'incubation. On présente d'autres informations sur les variations de la reproduction (utilisation de spermatozoïdes frais v. spermatozoïdes emmagasinés) et les gradients du taux de fécondité selon la latitude. Certains faits révèlent qu'un grand nombre d'oeufs sont perdus pendant l'incubation, y compris la perte d'oeufs non fertilisés, à cause de la prédation, du parasitisme et du décollement.

Commentaires

- On présente des données inédites sur le succès de l'accouplement chez C. bairdi. Il semble que les mâles de >100 mm LC sont plus portés à s'accoupler avec succès avec des femelles primipares et multipares.
- On s'interroge sur la durée de vie des femelles multipares. On signale l'observation de la sénescence chez les femelles des eaux hauturières de l'est du Cap-Breton en l'absence d'un recrutement pendant plusieurs années.
- On traite de la capacité d'accouplement de mâles en phase préterminale d'après les résultats d'expériences menées dans les régions du Golfe et de Terre-Neuve.
- On étudie les caractéristiques permettant d'identifier les vieux spermatozoïdes et ceux récemment émis. On souligne que la présence de marques récentes d'une étreinte sur la carapace de la femelle peut révéler un accouplement récent.
- Quoiqu'on soit d'accord que les petits mâles peuvent peut-être s'accoupler avec des femelles multipares, on partage l'opinion qu'ils n'ont pas autant de succès quand ils sont en compétition avec des gros mâles ou qu'ils sont en présence de grosses femelles.
- En dernier lieu, on mentionne que ce sont les petits mâles qui s'accouplent avec les femelles primipares et les gros mâles avec les femelles multipares dans le cas de C. bairdi.

V. Répartition et migration

Sommaire

Le crabe des neiges se rencontre surtout sur des substrats vaseux ou sablonneux-vaseux à des températures variant de -0,5 à 5,0 °C. Les femelles matures et les individus immatures montrent une tendance élevée au groupement tandis que la répartition des gros mâles s'approche d'une distribution aléatoire d'après les résultats d'une première étude photographique. On observe souvent des juvéniles immatures sur des substrats vaseux-graveleux en eaux peu profondes. Des données révèlent qu'ils migrent vers des substrats vaseux profonds quand ils atteignent la maturité. On observe souvent des petits juvéniles sur les mêmes substrats vaseux fréquentés par les adultes.

Une analyse statistique de la distribution des effectifs selon la taille étaye l'hypothèse d'un recrutement annuel aux pêcheries en deux vagues, une composée de crabes qui atteignent la taille légale par suite de la mue qui a lieu dans les pêcheries et l'autre composée de crabes qui migrent vers les pêcheries plus tard au cours de la saison.

a) Migrations locales : Elles semblent liées à l'intensité de la lumière, les crabes étant plus actifs à la noirceur.

b) Migrations à grande échelle : Selon les résultats de plusieurs études d'étiquetage menées dans l'est du Canada, la plus grande partie des crabes de >95 mm LC parcourent moins de 25 km entre le moment de l'étiquetage et de la capture. Une analyse plus poussée des migrations en fonction de la durée de la période de liberté et de l'endroit d'étiquetage est nécessaire. Ces migrations semblent non orientées. Toutefois, quelques observations comme les études sur la migration d'accouplement dans la Baie-Bonne portent à croire à l'existence de migrations saisonnières orientées.

À part la dispersion pendant la période larvaire, il est peut probable qu'il existe un important mélange entre les différents groupes de crabes dans les eaux de l'Atlantique canadien.

Commentaires - On avance l'hypothèse que la distribution des groupes peut être expliquée en fonction d'interactions sociales-écologiques comme l'exclusion des petits crabes par les gros individus.

- On tente de déterminer si des facteurs écologiques comme la présence d'abris et de sources appropriées de nourriture pourraient expliquer la présence de petits juvéniles sur des substrats hétérogènes et de gros crabes sur les substrats vaseux.

- On signale que la télémétrie par ultra-sons représente un des outils les plus appropriés pour l'étude des migrations à petite échelle quoiqu'elle soit relativement coûteuse.

- On note que l'échelle de la répartition des étendues de substrats qui pourraient être étudiées à l'aide de photographies et de vidéos ou d'un sonar à balayage latéral a une incidence directe sur l'interprétation de la répartition et des migrations à petite échelle des crabes de toutes tailles.

- Les résultats générés par la méthode d'étiquetage traditionnelle sont limités et ne concernent que les déplacements nets entre la date d'étiquetage et la date de recapture.

- On explique que par le passé, la plupart des études d'étiquetage étaient axées vers la détermination des effectifs et non vers la détermination des migrations.

- On mentionne que les migrations limitées des crabes pendant les saisons de pêche par rapport aux régimes spatial et temporel d'exploitation par la flottille peuvent entraîner un biais des résultats de l'analyse de Leslie.

VI. Mortalité naturelle

Les diverses espèces de crabes sont exposées à de nombreuses sources de mortalité au cours des différentes phases de leur cycle vital. Les oeufs sont vulnérables à l'abrasion mécanique, aux parasites et aux maladies. La variation du taux de mortalité est probablement plus élevée au stade larvaire. La survie des larves peut dépendre de conditions océanographiques variables, de sources appropriées de nourriture, de la prédation limitée et des conditions du milieu de vie benthique.

Les crabes juvéniles et adultes sont la proie de nombreuses espèces (jusqu'à 14 en Alaska). Dans l'est du Canada, la morue et la raie sont les principaux prédateurs. La quantité de crabes consommés par des prédateurs a été déterminée dans certaines régions pour une période limitée mais elle varie en fonction de nombreux facteurs écologiques. L'incidence de la prédation comporte aussi une forte composante saisonnière. De plus, on a observé un certain cannibalisme.

Les crabes peuvent être l'hôte de plusieurs organismes vivant en symbiose notamment des champignons, des bactéries, des bryozoaires, des hydraires, des polychètes, des bdellaires et des anatifes. Leur incidence sur le taux de mortalité annuel est probablement négligeable. Il existe aussi d'autres sources de mortalité par pêche indirecte comme la pêche au filet maillant, le chalutage, la pêche par casier abandonné et le traumatisme entraîné par la mauvaise manutention des petits crabes par les pêcheurs.

Commentaires - Les estimations actuelles du taux de mortalité naturelle du crabe des neiges des eaux de l'est du Canada sont arbitraires.

- Le taux de mortalité varie probablement selon le stade du cycle vital mais on doit considérer que la variation peut être importante au sein d'un stade, entre les individus et entre les différents groupes et individus selon les conditions environnementales subies.

- On souligne que la survie des juvéniles est probablement limitée par le nombre d'habitats adéquats disponibles qui peut être un facteur limitatif du recrutement.

- Il serait opportun d'effectuer des recherches sur la mortalité des oeufs surtout celle entraînée par les prédateurs.

VII. Modélisation

On présente un modèle basé sur de simples hypothèses *a priori* qui décrit la distribution des crabes selon les classes de mues. Quand le taux de mortalité naturelle baisse en fonction de la taille, l'incidence de la pêche est nettement marquée. On observe qu'un stock vierge regroupe des animaux de grande taille qui montrent un faible pourcentage de mue. La capture d'animaux de taille légale réduit le stock actuel de gros individus par un facteur supérieur à 10 et amène une augmentation de la proportion de crabes qui muent.

On présente des estimations du rendement tirées d'un modèle de rendement d'équilibre où les petits crabes ne s'accouplent pas. On a aussi obtenu des estimations du rendement quand seuls les crabes en phase terminale se reproduisent. On voit ainsi que le stock modélisé ne réagit fortement à l'exploitation que si les gros mâles en phase terminale se reproduisent. Les cycles du rendement dans des simulations dynamiques ne sont réduits que si les mâles en phase terminale se reproduisent.

Les résultats générés par ce modèle portent à croire que le taux d'exploitation actuel élevé dans les pêcheries de l'Atlantique et de la mer de Béring, qui va de 60 à 80 %, ne s'accordent pas avec l'unique fait que les gros mâles en phase terminale se reproduisent.

Commentaires - On souligne que le modèle montre qu'un potentiel reproducteur adéquat ne garantit pas un recrutement adéquat à la pêche.

- On indique qu'il n'est pas nécessaire d'utiliser des modèles sophistiqués pour prédire le meilleur rendement par recrue à des taux d'exploitation élevés étant donné l'abondance de crabes en phase terminale dans la pêcherie. Afin de maximiser le rendement, il est inutile de laisser dans la pêcherie des animaux dont la croissance a cessé sauf peut-être pour la reproduction.

- Le point précédent entraîne une discussion sur les données disponibles sur la croissance du crabe des neiges qui peuvent servir à l'élaboration de tels modèles. On mentionne qu'on dispose de peu de données sur les intervalles de mue. Malgré tout, on note que la fréquence des mues dans une classe de taille donnée est une approche pratique au problème.

- On discute de la pertinence de l'élaboration de tels modèles en l'absence d'importantes données détaillées mais les auteurs indiquent que les modèles aident à identifier les variables les plus sensibles.

VIII. a) Croissance et mue

i. Est-ce que la croissance continue chez les mâles après l'acquisition de la maturité sexuelle?

Les participants examine quatre types d'information qui étayent l'argument selon lequel les mâles continuent à muer :

1. Les ouvrages publiés mentionnent que chez les groupes d'individus de grande taille, il semble y avoir une baisse du taux de fréquence des mues mais qu'il y a une ou deux mues après l'acquisition de la maturité.

2. Selon des données inédites recueillies de 1974 à 1987 dans la mer de Béring, il semble exister une mue annuelle qui touche de 80 à 90 % des individus. Elle n'a toutefois pas eu lieu en 1980 et 1982, années où la mue semble avoir été retardée jusqu'à l'année suivante dans le cas des gros animaux.

3. Analogies entre congénères : On a observé en laboratoire l'accouplement et la mue ultérieure de mâles de C. bairdi; de plus, 87 % des femelles matures (dont la mue terminale est universellement reconnue) échantillonnées portaient des anatifes tandis qu'aucun des 2 000 mâles observés au cours de l'étude n'en portait.

4. On a observé des lésions bactériennes sur la carapace de femelles de C. tanneri mais non chez les mâles malgré le fait que cette espèce ne fait pas l'objet d'une exploitation commerciale. Ceci porte à croire à l'absence d'une mue terminale après l'acquisition de la maturité chez les mâles de C. tanneri.

Il existe dans le mer de Béring des régions où sont présents de grands nombres de mâles à vieille carapace.

ii. À l'acquisition de la maturité sexuelle, est-ce que les crabes sont de tailles variables et subissent-ils une mue terminale?

Selon les données présentées, les mâles de C. opilio cessent de muer après l'acquisition de la maturité. Il souligne que la plupart des études qui semblent indiquer l'existence d'une telle mue sont basées sur des observations préliminaires présentées dans un vieux document japonais et que les halieutes ont utilisé un seul repère pour définir l'état de maturité. Cette méthode peut avoir été efficace dans le cas des populations préexploitées où il existait une démarcation nette des tailles entre les individus matures et immatures. Toutefois, avec l'avènement de la pêche, l'abondance relative selon la taille a changé et, dans la situation actuelle, les tailles des mâles en phase préterminale et terminale se chevauchent.

Une mue terminale peut avoir lieu à un grand écart de taille et, peut-être, d'âge. On présente des données scientifiques qui permettent d'identifier les mâles en phase terminale, les mâles en phase préterminale porteurs de gonades matures et les juvéniles. On conseille la réalisation d'études visant à comparer la répartition des tailles chez ces divers groupes de mâles.

On a mentionne que l'organe Y est responsable de la sécrétion d'une hormone prémue et d'un facteur nécessaire à l'exuviation. Toutes les données publiées sur les Majidés indiquent que la mue de puberté représente la mue terminale qui est suivie de l'atrophie ou de la perte de l'organe Y.

On a remarque qu'il y a au moins transformation, sinon dégénérescence, de l'organe Y après la mue terminale. On attend l'achèvement de l'étude avant de formuler des conclusions définitives.

Discussion : L'existence d'une mue terminale au moment de la puberté chez le crabe des neiges mâle du golfe du Saint-Laurent fait l'objet d'un accord commun. Ceci concorde avec toutes les observations réalisées sur de nombreuses autres espèces de Majidés. Il incombe maintenant de prouver qu'une mue terminale n'existe pas dans les autres secteurs. Les données présentées sur les mâles de Chionoecetes opilio de la mer de Béring, quoique non concluantes, portent à croire qu'ils continuent à muer à toutes les tailles et que le potentiel reproducteur du stock est maintenu. On a besoin d'autres données morphométriques et histologiques afin de vérifier l'existence d'une mue terminale au moment de la puberté chez les mâles de la mer de Béring.

Toutefois, la mue terminale ne coïncide pas forcément avec la puberté chez les mâles de C. bairdi. Des nombres élevés de mâles muent après s'être accouplés avec succès. Cette question demeure toujours sans solution dans le cas de C. opilio du Pacifique.

Des données recueillies sur C. opilio de la mer de Béring concordent avec une mue terminale si les animaux sont uniformément pêchés après cette dernière mue.

b) Variables qui influent sur le recrutement

i. On examine les données qui étayent ou annulent l'hypothèse nulle selon laquelle la pêche n'a eu aucune incidence sur le niveau de recrutement à la pêche commerciale.

ii. On examine des données qui étayent ou annulent l'hypothèse nulle selon laquelle des facteurs liées à la densité n'ont aucune incidence sur le niveau de recrutement annuel à la pêche commerciale du crabe des neiges.

iii. On examine des données sur les influences potentielles de facteurs non liés à la densité sur le recrutement.

iv. On présente une hypothèse, basée sur des quantifications physiologiques expérimentales, selon laquelle la croissance et la reproduction peuvent être dangereusement limitées par la température de l'eau et donc que la migration des crabes en réaction à la température ambiante peut porter un certain avantage.

Discussion

On indique que la présence de juvéniles en eaux peu profondes peut être un phénomène lié à la température. On remarque que la migration en réaction à la température de l'eau devrait faire l'objet d'études sur le terrain par étiquetage électronique. On note que des femelles étiquetées après l'accouplement dans la Baie-Bonne et dans la mer du Japon ont migré vers les eaux côtières moins profondes et plus chaudes; un tel comportement peut influer sur les taux de développement des oeufs. On recommande la réalisation d'autres études physiologiques dont les résultats pourraient expliquer certaines des observations écologiques. On souligne que la plupart des crabes peuplant les eaux de l'est de Terre-Neuve ne peuvent pas éviter leur habitat thermique en migrant vers des eaux plus profondes car ils fréquentent déjà des profondeurs maximales.

Ce dernier point sert d'argument pour étayer l'hypothèse selon laquelle la croissance et le recrutement à la pêche de Terre-Neuve sont limités par la température. Des observations expérimentales inédites révèlent que l'éclosion de oeufs et le développement larvaire ont lieu à des températures allant de -2 °C à 2 °C. Selon des données expérimentales publiées, le crabe des neiges mue à une température variant de 0 °C à 1 °C. On souligne toutefois que de telles observations doivent tenir compte du nombre de degrés-jours accumulés.

On présente des arguments à l'effet que l'effondrement des stocks de crabe des neiges de l'est du Cap-Breton ne devrait pas être interprété comme un phénomène résultant de la pêche. L'effondrement peut avoir été le résultat de l'absence de dispersion des larves dans cette région et de l'existence d'habitats marginaux.

On présente des questions sur l'abondance des juvéniles du crabe des neiges. On signale qu'il y a un nouvel influx de prérecrues dans la Baie-Bonne comme c'est le cas pour le crabe des neiges de l'est du Cap-Breton, le crabe royal de la mer de Béring et le crabe dormeur. On croit que le recrutement est sporadique dans de nombreuses pêcheries du crabe.

On présente les deux hypothèses vérifiables suivantes :

1) La capture de gros mâles en phase terminale mène à une augmentation du taux de croissance ou du recrutement de petits mâles à la pêche.

2) La capture de gros mâles a une incidence sur le taux de fécondité de la population. On peut vérifier ceci en observant le nombre relatif d'oeufs fertilisés et l'incidence de femelles ovigères.

En ce qui concerne la deuxième hypothèse, on mentionne que des données inédites révèlent que les taux de décomposition des oeufs aux basses températures signalées dans les pêcheries du crabe des neiges sont faibles et que les oeufs non fertilisés peuvent survivre jusqu'à 11 semaines.

La discussion porte sur la relation douteuse entre le niveau de fécondité de la population, l'abondance des larves et le recrutement ultérieur. Quoiqu'on ait observé chez d'autres espèces que des niveaux de fécondité relativement faibles peuvent générer d'importantes classes annuelles, on devrait étudier la possibilité que l'exploitation de C. opilio est concentrée sur une seule classe annuelle. Étant donné les taux de capture actuels, le taux de fécondité de la population peut être l'objet d'une influence négative.

On présente le revers de l'argument, c'est-à-dire que les femelles pourraient tirer avantage de l'exploitation des mâles étant donné qu'elles disposeraient ainsi de plus de nourriture et d'habitats.On tente de déterminer si les taux de capture au casier traduisent exactement les régimes d'abondance et l'importance du recrutement. Les données recueillies sur la pêche au casier peuvent fournir des indices utiles de l'abondance mais l'on doit considérer d'autres facteurs comme le régime de pêche temporel et l'emplacement précis des lieux de pêche.

On répète les arguments selon lesquels l'intensité de la pêche dans le golfe du Saint-Laurent n'a été élevée qu'au cours des cinq dernières années. Il est donc prématuré de prévoir la manifestation d'influences négatives sur le taux de fécondité de la population en ce moment. Certes, il semble assez évident que le taux de fécondité actuel n'est pas forcément entièrement protégé par l'imposition d'une taille légale de 95 mm LC. Quoique cette observation ne signifie pas forcément qu'il existe un problème, elle révèle qu'on doit toutefois être prudent.

On recommande que le taux de fécondité des femelles fasse l'objet d'une surveillance régulière qui comprendrait l'examen de la condition des spermatothèques et des gonades.

Des données portent à croire que le taux de croissance et de survie ont varié à cause de la pêche, c.-à-d. qu'en l'absence d'une exploitation, la présence de mâles en phase terminale peut avoir ralenti la croissance des mâles en phase préterminale ou réduit leur survie. Il semble que les mâles en phase préterminale sont relativement plus abondants actuellement par rapport à la période de préexploitation.

On a longuement discuté la question des tendances du taux de capture et de la production ainsi que l'incidence potentielle de la pêche sur ceux-ci. On a souligné à nouveau qu'on ne disposait d'aucune donnée qui prouvait que la pêche avait eu une incidence sur le recrutement jusqu'à maintenant.

On traite des mécanismes possibles responsables de l'acquisition, chez les mâles, de la maturité à une petite taille et de la baisse du nombre relatif de gros mâles. On s'accorde en général pour dire qu'on ne dispose pas de données suffisantes pour rejeter l'hypothèse nulle selon laquelle la pêche n'a eu aucune incidence sur le recrutement aux pêcheries.

On étudie les régimes de rendement et de pêche historique dans le golfe du Saint-Laurent. On tente de déterminer si la situation actuelle représente l'élimination d'un stock vierge par pêche ou si le stock vierge a été éliminé dans les années 1970. Toutefois, on reconnaît que des données précises et exactes sur l'emplacement des lieux de pêche sont essentielles à la réalisation d'études futures. De plus, on propose que la pêche expérimentale est peut-être la seule méthode qui permettrait de trouver une réponse aux questions relatives à l'incidence de la pêche sur les niveaux de recrutement.

On reconnaît que l'utilité des données sur la fréquence des tailles et la condition de la carapace est limitée. À l'avenir, les chercheurs devraient compléter ces données à l'aide d'information sur les stades de mue, les caractères morphométriques, la viabilité des oeufs et l'emplacement précis de pêche ainsi que d'échantillonnages des prises en mer.

À nouveau, les arguments pivotent sur la "préoccupation" soulevée par les niveaux de fécondité du crabe des neiges. On est loin de s'entendre sur la gravité de ce problème.

On examine la relation entre la poussée phytoplanctonique printanière et la survie des larves. Dans le même ordre d'idées, on se penche sur la survie des autres stades vitaux. On est d'accord que le "stade du cycle vital critique" varie probablement d'une année à l'autre et donc que la prédiction du recrutement est forcément une opération complexe. Toutefois, l'abondance des juvéniles avant le recrutement devrait faire l'objet d'une étude par chalutage tout comme les facteurs qui influent sur la survie et la dispersion des larves.

En conclusion, on ne semble pas disposer d'assez de données pour accepter ou rejeter les hypothèses nulles sur les incidences liées à la densité ou non. On identifie les lacunes critiques des connaissances nécessaires à l'explication de ces questions.

IX. Résumé de l'historique de l'exploitation

Le développement de la pêche du crabe des neiges dans l'Atlantique canadien a eu lieu au cours des 20 dernières années. L'analyse des statistiques sur les prises commerciales, y compris les données provenant de bordereaux d'achat et de journaux de bord, et des résultats de recherche visant à déterminer l'abondance et d'autres paramètres biologiques sert au contrôle de la situation du stock et des activités de pêche. À l'origine, la réglementation n'était basée que sur des questions de transformation.

L'utilisation du chalut était interdite afin de minimiser les dommages à l'habitat et au crabe. À cause de leur petite taille, les femelles n'étaient pas pêchées; seuls les gros mâles (>100 mm LC) étaient considérés comme exploitables. Par la suite, la limite de taille a été portée à 95 mm LC au moment où l'industrie devint capable de transformer les petits crabes.

Vers le milieu des années 1970, on adopta des dispositions visant une baisse de l'effort en limitant l'accès à la pêche ainsi que le nombre de casiers. L'augmentation des prises vit l'établissement de zones et l'octroi de l'accès exclusif à un nombre limité de pêcheurs locaux. Dans le cas de la pêche côtière, on prévoyait que l'exploitation du crabe ne serait pas l'unique source de revenus pour les pêcheurs mais que ceux-ci participeraient à d'autres pêches. Dans quelques zones, on fixa un total des prises admissibles (TPA) préventif et on établit un contingent pour chaque bateau. Au début, les TPA étaient basés sur l'augmentation prévue de la biomasse moyenne annuelle (Cap-Breton), puis sur 50-60 % de la proportion exploitable de la ressource (Terre-Neuve) et enfin sur les tendances historiques de la pêche (sud-ouest du golfe).

Le déploiement de la pêche vit une augmentation du nombre relatif de crabes à carapace molle entraînée par la pêche pendant la période de mue. Afin de pallier à ce problème, on adopta des dispositions visant à interdire la pêche pendant l'été. Afin d'éliminer la capture de crabes de taille non légale, on adopta une disposition fixant le maillage minimum des casiers.

Dans la situation idéale, les gestionnaires aimeraient obtenir du CSCPCA des estimations précises des effectifs de chaque stock. Ils aimeraient aussi connaître le moment de la mue, les limites précises du stock et les prises annuelles maxima qui pourraient être permises sans menacer l'existence de la pêche.

Ces données ne sont pas disponibles pour tous les stocks; par conséquent, les échanges relatifs aux TPA sont parfois difficiles et les différences d'opinions difficiles à résoudre. Le CSCPCA doit souvent fournir des conseils basés sur des hypothèses arbitraires. Une conjecture est considérée plus utile qu'aucune estimation.

X. Incidence des facteurs biologiques sur la gestion

On résume les données biologiques présentées dans le contexte de la gestion ainsi que leur pertinence et leurs lacunes en termes des options d'exploitation futures. On signale que les débarquements provenant de différentes zones de gestion ont soit baissé, augmenté ou resté stables. Il est difficile de déterminer s'il existe un régime régional global. Selon des observations générales, les dernières pêches ont eu tendance à dépasser les taux d'exploitation recommandés. Dans certains cas, ceci peut avoir entraîné un déclin général de l'abondance. On a aussi noté une augmentation du nombre de crabes à carapace molle et de crabes de taille sublégale dans les prises. Étant donné ces facteurs, la capacité de reproduction de la population peut ne pas être protégée par la réglementation actuelle. Vu la baisse relative de l'abondance de gros crabes, l'exploitation annuelle ne porte en grande partie que sur les recrues de l'année et la capacité de tampon permettant d'alimenter des débarquements annuels comparables peut être réduite. Les débarquements futurs dépendront en grande partie sur le niveau de recrutement à la pêche de l'année en cause.

D'après nos connaissances actuelles de la biologie du crabe des neiges et par suite de l'acquisition d'autres donnés sur la croissance, on pourra modifier le taux de mortalité cible par pêche selon la classe de taille et on pourra recommander une baisse des débarquements. Il serait peut-être aussi désirable d'y associer une exploitation intermittente des pêcheries et la rotation de la pêche entre les pêcheries afin de réduire la mortalité par pêche et d'établir un grand nombre de classes d'âge (=de taille?) exploitables. Il serait peut-être avantageux de permettre aux pêcheurs d'exploiter les petits crabes en phase terminale dans le cadre d'une pêche intermittente qui ferait l'objet d'une limite de taille minimum de la pince au lieu d'une limite de la largeur minimum de la carapace. Il n'est pas évident pourquoi la reproduction de la femelle devrait être maintenue à 100 % étant donné qu'aucune relation stock-recrutement n'a été établie et que le crabe représente un cas d'exploitation unique vu que les femelles sont sous-exploitées. On doit encore déterminer si la surpêche au détriment du recrutement pose vraiment un problème. Les migrations relatives du crabe par rapport à la flottille de pêche peuvent compromettre l'utilisation du modèle de Leslie pour l'évaluation des stocks. Le perfectionnement des estimations du taux de mortalité naturelle selon la taille peut aussi influer sur les décisions concernant la classe de taille cible étant donné que la mortalité naturelle s'accumule à la mortalité par pêche.

On propose les priorités de recherche suivantes :

1) Croissance - Les données disponibles doivent être résumées et les régimes et taux de croissance, mieux documentés. On doit établir l'âge estimatif des recrues à la cohorte en phase terminale pour la modélisation des populations et la détermination du potentiel de surpêche au détriment de la croissance.

2) On a besoin d'une méthode fonctionnelle indépendante de l'exploitation pour établir l'abondance des prérecrues mâles.

3) La qualité des données sur les prises et l'effort doit être améliorée en termes de l'intégralité et de la nature des données recueillies. Ces données sont plus importantes pour les comparaisons inter-annuelles que pour les comparaisons intra-annuelles et sont nécessaires pour déterminer les tendances de l'abondance des effectifs dans le cadre de l'évaluation de l'incidence de la pêche sur les ressources.

4) On devrait déterminer le rôle des mâles en phase terminale de < 95 mm LC dans le processus de reproduction étant donné la baisse générale de l'abondance de gros mâles et la surpêche future potentielle au détriment du recrutement.

Commentaires : - D'après les données limitées présentées, il semble que la pêche peut avoir une incidence positive sur l'abondance des juvéniles. Si c'est le cas, nous avons besoin des données suivantes :

a) les taux de croissance et de mortalité naturelle des mâles de >70 mm LC;

b) le pourcentage d'individus de chaque classe de taille qui atteignent le stade larvaire terminal après mue.

Ces données permettraient de formuler des recommandations quant au rendement par recrue de crabes de >70 mm LC en fonction de différents taux de mortalité par pêche et de limites de taille minimum.

II - REVIEW OF SNOW CRAB BIOLOGY

A. Stock Definition and Larval Mixing in the Snow Crab, (*Chionoecetes opilio*)

by R.W. Elner

INTRODUCTION

Snow crab, *Chionoecetes opilio* (O. Fabricius) are found in deep, cold water in the Northwest Atlantic and North Pacific Oceans and the Sea of Japan. Off the east coast of North America, snow crab are distributed from West Greenland to Maine (Squires 1966) from 20 to 700 m depth. Currently in Atlantic Canada, fishing grounds for snow crab extend along the east coast of Newfoundland, through the estuary and Gulf of St. Lawrence, and around Cape Breton Island. The various inshore and offshore grounds are partitioned into management areas based on fishery considerations (Bailey 1983; Parsons et al. 1983; Rowell 1983) rather than on biological criteria. For the purposes of this paper, a stock is defined as "a population of organisms which, sharing a common gene pool, is sufficiently distinct to warrant consideration as a self-perpetuating system which can be managed" (Larkin 1972).

The delineation of stocks and the mechanics of stock-recruitment relationships are problems fundamental to fisheries science. An underlying assumption is that if stocks can be identified, then effective management regimes can be imposed to optimize exploitation of the resource. Ennis (1986) detailed five requirements for determining a stock-recruitment relationship:

1. a population that is more or less discrete, both geographically and biologically (i.e., a stock);
2. measure of stock size over a time period when abundance ranged widely;
3. measure of recruitment to the stock which coincides with the same time period;
4. an understanding of the effect of variation in factors other than stock size on recruitment variability; and,
5. an understanding of recruitment processes for the stock.

Although components of all five requirements have been studied for C. *opilio*, there has been no concerted attempted to integrate results and re-define management areas. Indeed, Davidson et al. (1985), after broadly identifying various phenotypic and genetic snow crab stocks and reviewing their fishery dynamics, concluded that a phenotypically and/or genotypically defined stock is not necessarily a useful management tool. Stocks may be more usefully subdivided into practical management units that reflect intra-stock variation in factors such as growth and recruitment.

In snow crab, as for most commercial invertebrates, critical linkages between oceanography and larval life history phases are lacking. Hence, there is only scanty understanding of both sources of recruitment and larval mixing. There has thus been little progress in understanding temporal and spatial variability in recruitment patterns or in establishing reliable predictive models. With larval mixing, it is important not to lose appreciation of the population or stock as an entity in itself. It is obviously critical to the continuity of the stock in time and in space for either the larvae or a later-life history phase to complete the genetic cycle by returning to the brood areas. As reviewed by Jamieson (1986), egg hatching locations are often geographically removed from habitats favourable for survival of juveniles, which, in turn, may differ from areas preferred by adults. If a species has not evolved a reproductive strategy to return larvae or juveniles to areas of adult abundance (fishery grounds) on a regular basis, then the stability of the stock cannot be assumed and it will be practically impossible to predict recruitment.

The present paper provides a synthesis of stock definition and larval mixing studies on snow crab.

Stock Definition

The delineation of management units for invertebrates species, based on an understanding of stock structure and distribution, has been posed as the most critical question facing fisheries management in the Atlantic Zone (Sinclair et al. 1987). Although various approaches have been applied to stock delineation problems, the use of multivariate statistical comparisons of morphological and meristic characteristics and electrophoresis have gained acceptance among fisheries scientists (Saila and Flowers 1969; Parsons and Hodder 1971; Johnston et al. 1974; Messieh 1975; Smith et al. 1980; Mulley and Latter 1981). Using such techniques, differences are used to infer phenotypic and/or genotypic distinctions between individuals. To date, most stock delineation studies on decapod crustaceans in the Northwest Atlantic have been restricted to the American lobster, Homarus americanus, and have met with limited success (Saila and Flowers 1969; Barlow and Ridgeway 1971; Tracey et al. 1975; Campbell and Mohn 1982; Ennis 1986). Prior to Davidson (1983) and Davidson et al. (1985), the only study to have used morphometrics for investigating snow crab stocks was by Kanno (1972), who utilized analysis of co-variance to compare 13 morphometric characteristics between fishing grounds in the Okhotsk Sea.

Davidson (1983) and Davidson et al. (1985) compared morphometric, meristic, electrophoretic and fecundity characteristics for snow crab from sampling areas off St. John's, Newfoundland, eastern Cape Breton Island, western Cape Breton Island, and in the western Gulf of St. Lawrence. Discriminant function analyses of the morphometric, meristic and fecundity data indicated that snow crab from the four areas were morphologically and biologically distinct. Differences in morphology were proposed as being largely due to environmental effects on growth of juveniles. However, the maturity of the male crabs sampled was determined from previously published size at maturity information (Watson 1969, 1970). Unfortunately, recent studies (Conan and Comeau 1986) have found morphologically immature males considerably larger than the maximum size threshold used by Davidson et al. (1985), and it is possible that inter-area variations in the proportion of morphologically immature males sampled, coupled with allometric growth relationships (Conan and Comeau 1986), may have created biases. Electrophoretic data suggests that Newfoundland and western Gulf of St. Lawrence snow crab differ genetically from each other and from Cape Breton Island crabs (Davidson et al. 1985). Eastern and western Cape Breton Island snow crabs did not exhibit electrophoretic differences and thus, appear to represent a single genetic stock.

Given the 71-day pelagic larval duration period estimated for C. opilio and prevailing summer surface circulation patterns, Davidson et al. (1985) hypothesized that it is possible through larval dispersion for some genetic exchange to occur between all Atlantic snow crab populations.

Davidson et al. (1985) reviewed the applicability of the "single-stock-management-unit" concept by comparing the management histories of the two fishing areas within the Cape Breton Island snow crab stock. Since 1978, the management strategy for eastern and western Cape Breton Island snow crab grounds has been to develop a stable, supplementary fishery with a large number of participants (Elner 1982). Consequently, total allowable catch (TAC) restrictions in these areas were based on a strategy of permitting a harvest of biomass equivalent to estimated growth and recruitment additions to the commercial biomass for the previous year. Both areas were expected to respond similarly to this management strategy. However, within four fishing seasons, catch rate and commercial biomass in eastern Cape Breton greatly decreased (Elner and Robichaud 1985). In contrast, catch rate and commercial biomass have remained relatively stable in western Cape Breton Island (Elner 1982).

Evidence accrued from annual stock assessments indicates that recruitment to the commercial stock on eastern Cape Breton Island snow crab grounds is sporadic (Elner and Robichaud 1986; 1987). Davidson et al. (1985) hypothesized that there is little endemic larval recruitment onto the eastern Cape Breton Island grounds. Larvae released from this area may become entrained in local gyres or swept northeast towards Newfoundland, but the predominant surface currents in the area would tend to disperse pelagic larvae either south along the coast of Nova Scotia or offshore. Snow crab larvae are present throughout the Scotian Shelf, with early larval stages more abundant in the north. The megalopal stage has been found only in the south (Roff et al. 1984). This type of larval distribution, plus the presence of small numbers of snow crabs in the Bay of Fundy and in the Gulf of Maine, supports the possibility of a large southward loss of C. opilio larvae from eastern Cape Breton Island. Based on neuston larval collections on the Scotian Shelf, Roff et al. (1986) estimated that along-shore larval drift for snow crab zoea originating on the eastern Cape Breton Island crab grounds would be 3-11 km d^{-1}. Thus, the eastern Cape Breton Island snow crab population was probably established over time through occasional pulses of larval recruitment, probably from the western side of the island. Such a scenario would account for initially high catch rates and landings, a lack of resilience of the resource to exploitation, and the subsequent deterioration of biomass and catch rates after only a few fishing seasons.

In contrast with the east coast, larval recruitment appears to be more regular in western Cape Breton Island. Overall, annual biomass additions, although variable in magnitude, have appeared relatively large and consistent since 1978 (Elner 1982). Despite a high exploitation rate, this has conferred resilience on the western Cape Breton Island stock and has facilitated management.

The experiences of the Cape Breton Island snow crab fishery indicate that a "stock" per se, as defined by genetic and/or phenotypic characteristics, is not necessarily a meaningful management unit. Stocks may be more usefully subdivided into management units that reflect intra-stock variation in factors such as growth and recruitment. Thus, unique phenotypic and/or genotype characteristics of intraspecific groups of individuals may be useful in the delineation of stocks, but should not be accepted as a basis for management strategies until the biotic and abiotic factors governing these characteristics are elucidated.

Larval Mixing

Various studies have shown variation in the size structure of adult snow crab populations, which have been interpreted as being due to sproadic, strong year-classes which dominate the stock for several years (Somerton 1981; Elner and Robichaud 1987). Fluctuation in effective larval production (due variously to reproductive output of adult females, larval mixing patterns and larval survival) may be an important source of such variability. A fundamental lack of understanding about the movement and behaviour of brachyuran larvae, particularly in relation to ocean currents, appears to be the biggest single factor responsible for the present dearth of knowledge. With the notable exception of a multi-faceted study by Kelly et al. (1982) on dispersal of deep-sea red crab (*Geryon quinquedens*) larvae, there are few predictive transport models for crab larvae that combine understanding of larval behaviour and biology with oceanography. Larvae of *C. opilio* take at least 60-70 days to develop in the plankton (Davidson et al. 1985; Kon 1970) and therefore, could potentially be carried for considerable distances by ocean currents. However, the larvae of some brachyuran species have a pronounced diel vertical migration and the various larval stages may have their own peculiar depth distributions (Sulkin 1984, 1986). It may not be meaningful to consider them always as passive surface drifters and equate their transport to mean residual surface currents. During their pelagic phase, crab larvae could be subject to a wide array of temperatures, current speeds and directions, factors critically influencing their eventual settlement position. Indeed, there is evidence (see Ennis 1983; Sulkin 1984; for reviews) that some species of decapod larvae are capable of influencing their settlement location by utilizing behavioural (e.g. diel vertical migration) and hydrographic mechanisms to maintain their mean position or even move against surface currents.

Egg hatching in *C. opilio* is reported to occur from February to April in the sea of Japan (Ito 1967), with a peak in March. Kurata (1963) found that further north in the Okhotsk Sea, hatching occurs from May to July. The time of hatching is still later along the Pacific coast of Japan, where zoea do not appear until August and September (Kurata 1963). In the Gulf of St. Lawrence, hatching is reported to occur from late April to June (Watson 1969; Powles 1966). Differences in the time of appearance of the planktonic larvae appear to be due to differences in environmental conditions in the areas surveyed (see Adams 1979, for review).

Snow crab larvae develop through a brief prezoeal stage, two zoeal stages, and a megalopal stage (Kon 1970). Estimates of larval duration (Table 1) range from 2-8 months (Ito 1970; Kon 1970). Kon (1970) derived the following equations to express the duration of each zoeal stage as a function of temperature (T°C):

$$\text{Duration (days) zoea I} = 300.89/T^{1.1117} \quad \ldots(1)$$

$$\text{Duration (days) zoea II} = 367.45/T^{1.1619} \quad \ldots(2)$$

Based on laboratory experiments, Davidson (1985) found that it was reasonable to use Kon's equations to predict zoeal duration for C. opilio from Atlantic Canada. Although Kon (1970) did not determine a relationship between the duration of the megalops stage and temperature, he did determine that temperatures of 10.1-15.2°C are necessary for the successful moult of the megalops to the first juvenile crab instar, while lower temperatures (mean 9.6°C) maximize survival from the first to the second zoeal stage.

Incze et al. (1987) investigated the distribution of C. opilio and C. bairdi larvae for discrete depth intervals (300-120, 120-80, 60-40, 40-20, 20-10, 10-0 m) in the southeastern Bering Sea during 1980 and 1981. The larvae were patchily distributed, as is characteristic of plankton in general (Wiebe et al. 1973; Fasham 1978). The vertical distribution of each zoeal stage for each species was similar in both years. On average, 80% of the larvae were in the upper 20 m of the water column and more than 93% were in the upper 40 m. Data were insufficient to statistically test for abundance differences between depths of 20-10 m and <10 m, although no trends appeared obvious. A plot of mean proportion of zoeal stages I and II by depth for daylight against darkness showed only slight shifts in larval distribution. In contrast, on the Scotian Shelf, C. opilio larvae reveal a strong pattern in diel variation, being nearly thirty times more abundant in neuston and metre nets at night time than during the day (Roff et al. 1984). Catches in the dawn-dusk period tended to be intermediate between day and night catches. Data on monthly changes in the depth distribution of each larval stage for the Japan Sea (Kon 1980) reveal a deeper distribution pattern than that of Incze et al. (1987), with pronounced monthly inter- and intra-stage shifts.

Lanteigne (1985) sampled snow crab larvae at four depth ranges (0-10, 12-20, 24-40, and 48-80 m) in the Baie des Chaleurs, Gulf of St. Lawrence, during May-August, 1982. Larvae were distributed throughout the water column. However, in general, the 0-10 m depth zone had relatively fewer larvae (zoea I and II, and megalops) and highest abundances were encountered at various depths below 20 m. The spatial distribution of adult females corresponded with the general location of zoea I during May, but the larvae became increasingly dispersed with time.

In Kon's (1980) summary of the larval life-history of C. opilio, the prezoeae, just after hatching, swim and rise toward the sea surface due to phototaxis. However, as the duration of the stage is only about one hour, they may have developed to zoea I before arriving at the sea surface. Highest densities of zoeae I were in the 0-50 m depth range in an area corresponding to the sea-bottom location inhabited by a large number of adult females at a depth of 225-275 m. The area was also an upwelling area. Most zoeae I were collected from early in March to early in April, and zoeae II were collected from early in April to early in May. After moulting to megalopae, larvae went down below the thermocline (200-250 m) between the warm Tsushima current and the deeper, cold Riman current.

As reviewed by Adams (1979), Ito (1970) and Kon (1970) take opposing views on the lengths of time required for newly hatched larvae to migrate from their hatching depth to the sea surface and for megalopae to migrate to the sea bottom. Whereas Ito (1970) estimates that vertical movement is slow, Kon (1970) argues that movement is rapid and that temperature effects at intermediate depths have little influence on larval duration.

Incze et al. (1987), in the most comprehensive study to date on factors influencing the recruitment of *Chionoecetes* species, compared 1978-1981 abundance data on larval *C. bairdi* and *C. opilio* to information on adult female abundance and regional oceanography of the Bering Sea. Significant inter-annual variability in larval abundance was detected in three areas for *C. opilio* and in one area for *C. bairdi*. In two of the areas, a sharp decline in abundance of *C. opilio* larvae after 1979 could be accounted for by decreased adult female abundance. In the remaining area, 2 small larval year-classes of *C. opilio* (1980 and 1981) and one of *C. bairdi* (1980) occurred despite an abundance of adult females. In these latter cases, Incze et al. (1987) hypothesized that low zooplankton abundance and low water column stability had resulted in unfavourable feeding conditions and, hence, increased mortality of zoea.

Somerton (1982) examined evidence that sea ice may be important in determining *C. opilio* distribution and recruitment success. According to Somerton, survival of *C. opilio* larvae appears to be timed to a spring bloom of phytoplankton, initiated by melting sea ice. Larvae may be adapted to enter the plankton at the usual time of the ice edge plankton bloom, and when this bloom fails, either because ice is not present or other conditions are unsuitable, larval survival decreases. If this hypothesis is correct, then the distribution of high densities of *C. opilio* larvae is limited by the maximum extent of sea ice in April when the larvae enter the plankton. Although the ice hypothesis was proposed for *C. opilio* in the eastern Bering Sea, it may be applicable to other areas such as the northwest Atlantic.

Regarding larval dispersal, Ennis (1983) examined the effects of wind, and presumably surface current, direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland near-shore area. Although *C. opilio* is found in deep-water, larval stages were found in nearshore areas when there was an onshore wind and, except for a few individuals at 3 m depth, were found only at the surface. Snow crab larvae appeared to move seaward by surface currents when winds were blowing offshore; there was no indication of any compensating behaviour by the larvae to avoid being transported away from shore. Ennis (1983) proposed that *C. opilio* larvae could be carried seaward for considerable distances and yet still be returned, and since larval dispersal appeared the result of surface currents, recruitment magnitude was probably largely dependent upon wind direction during the period when settling larvae were in the plankton. In contrast, data on wind offered little insight to Incze et al. (1987) in interpreting patterns of larval abundance in relation to possible advection events. Years with similar wind patterns differed dramatically in larval distribution, and larval transport patterns did not appear to correspond with wind direction.

DISCUSSION

From this review, it is apparent that much information on larval behaviour and dispersal for C. opilio is contradictory. Moreover, while there is sound experimental background on some aspects of larval and adult biology, there is no data with which to precisely define stocks and understand larval dynamics.

On the available evidence, from decapod larvae in general and the limited data on snow crab, two mutually-exclusive hypotheses are tenable regarding larval recruitment processes in snow crab. The first is based on the assumption that larvae are passive drifters and, assuming they concentrate near the surface, are transported by surface currents. This hypothesis predicts that larvae which settle in an area originate upstream, the direction and distance depending on current velocity and temperature. The second hypothesis, based on the larvae undergoing vertical migrations on an ontogenetic and/or diel scale, is that larvae can utilize currents moving at different velocities and/or directions, and predicts that larvae may either maintain their position near their hatching grounds or otherwise be transported in pathways not predictable by the first hypothesis. Study is now required to specifically establish which dispersal hypothesis is most relevant for C. opilio.

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Table 1. Duration of larval stages for the snow crab, Chionoecetes opilio.

Prezoea (min)	Zoea I (days)	Zoea II (days)	Megalops (days)	Total larval period (days)	Temperature (°C)	Reference
40-60	19	20.4	27	63-66	12	Kon (1970)
-	24-25	24-25	28	76-78	10-11	Kon (1970)
-	28.9	-	-	-	8.2	Davidson (1983)
-	25.7 (16-29)	10-8	34.5	71	11.0	Davidson (1983)
-	32-46	42	-	-	-	Lanteigne (1985)
-	27	27	-	-	-	Yamohara (1969)
-	30	30	90-180	150-240	-	Fukataki (1969)
-	-	-	-	210-240	-	Ito (1970)

B. Growth and Maturation of Snow Crab (Chionoecetes opilio)

by

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INTRODUCTION

Only male snow crabs (Chionoecetes opilio) are harvested in Atlantic Canada. A minimal legally harvestable size of 95 mm carapace width (CW) has been enforced since 1973. This is the smallest size acceptable by processors for meat extraction. It has frequently been assumed that snow crab stocks were protected from recruitment overfishing because the females were not harvested and because all males were thought to mature and have the opportunity to mate before they reached this minimal legal size (Powles 1968; Watson 1970). Females could mate only once, shortly after their last (terminal) moult to maturity; a female would thereafter use spermatophores stocked in her two spermathecae for fertilizing eggs over several broods in successive years. Furthermore, a single male seemed to have the potential to mate with several females as per aquaria observations. It has also been assumed that 95 mm CW was an acceptable minimal legal size for preventing overfishing. It was generally believed that all male C. opilio have the potential to grow until they reached an asymptotic size equivalent to the maximum sizes observed in the catch (130-140 mm CW). Notwithstanding, most Chionoecetes fisheries which have been managed under such assumptions showed an initial rapid increase in landings followed by an unpredicted decline, we believe that initial optimistic forecasts of high and stable yield may be explained by an unforeseen decrease in individual growth resulting from terminal moulting at the onset of the differentiation of secondary sexual characters for both males and females. Our recent observations suggest this alternative interpretation of their life history may lead to revision of the management strategy for snow crab stocks.

GROWTH

The traditional interpretation of the life history of the genus Chionoecetes is based on the general principles usually accepted for decapod crustaceans, which differs from that generally accepted for other genera in the majid crab family. The genus Chionoecetes pertains to the majid family of Oxyrhyncha Decapoda; other members of this family include the genera Maia, Pisa, Acanthonyx, Libinia, Hyas, and Macropodia. We shall present the general view of growth in decapod crustaceans, and then contrast the traditional and our recent understanding of that for Chionoecetes.

Growth in decapod crustaceans

The process of growth through moulting is discontinuous, i.e. growth in length proceeds stepwise. Complex hormonal changes occur during a moult cycle. The increase in actual meat weight proceeds less stepwise than the increase in size because body tissues are synthesized between actual moulting events.

The individual moult cycle of adult decapods does not occur at random over time (Conan 1985) and moult cycles are in phase with seasonal fluctuations in the environment according to species specific patterns. In a given region, moulting tends to occur at a similar time for all individuals sharing similar sex and age characteristics which are capable of moulting in a given year. The moult period matches fluctuations in the environment such as seasonal variations in temperature. It appears that most crabs in an area tend to moult simultaneously while even a few kilometres away, moults may be delayed by a few days to a few weeks. It has been suggested (Reaka 1976) that there may be communication between individuals in order to phase moult events. The time interval between successive moults usually increases as a function of age but when they take place, moults tend to occur during moulting periods. Large decapods moult infrequently once they reach an old age (large lobsters may moult once every 10-15 years). Young individuals may moult as frequently as weekly or monthly, and so their moulting schedules usually differ from those of adults. Young individuals over a small geographic area still tend to synchronize their weekly, bimonthly, or monthly moults. They will also preferentially moult at a fixed time of the day or night (Reaka 1976; Conan 1985; J. Kittaka, Kitasato University, Sanriku-Cho, Iwate-Ken, Japan, pers. comm.). Tidal, lunar, and semilunar periodicities have been described as synchronizing factors in the timing of moulting of juvenile decapod crustacea.

The periodicity in moulting can be studied by sampling the occurrence of moulting events in a population. The duration of moulting for an individual, however, is quite short and individuals tend to hide while moulting. Catchability varies as a function of the moult cycle. It is therefore preferable to sample intermoult, premoult and postmoult stages within the population as described by Drach (1939) and Drach and Tchernigovtzeff (1967). Moult stage can be established easily by observing epidermal development in transparent body parts (e.g. pleopods, epipedites). Moriyasu and Mallet (1986) defined three moult periods (post, inter, and premoult) and some stages and sub-stages based on their observations of morphogenesis of setae in the endite of the maxilla of snow crabs. Additional cross-checking can be done by histology, if required (Mallet and Moriyasu, unpub. data).

The increment in size at moult usually varies as a function of size and/or age. Linear models have been used to relate both size increments to initial size and postmoult size to premoult size. Changes in slope and elevation of these linear relationships may occur at different stages of maturity although it has also been stated that the changes are simply progressive and that the regressions used should be curvilinear rather than linear (Mauchline 1976).

Moulting and reproductive cycles are usually phased in timing. Normally, females about to spawn or already carrying eggs will not moult although exceptions to this rule have occasionally been described [e.g., in Homarus (Aiken and Waddy 1980)].

Moulting and reproduction are both controlled by hormones but the hormonal control of moulting is not rigidly coordinated with either the control of spawning or gonadal activity. Moulting is dependent on the presence of crustecdysone, a hormone whose synthesis is related to the activity of the Y-organ. Regeneration of missing limbs is also dependent on the presence of crustecdysone.

The combination of size increment at moult, the seasonal and diel timing of moulting, and the time intervals between moults of crabs of different age or size generates a stepwise curve relating average size to age of a cohort (Conan 1978). The curve usually flattens towards an asymtote with average size at the oldest ages. The curve representing average weights is also stepwise but less pronounced because growth in real meat weight occurs mainly between moults when tissue replaces the water pumped into the new exoskeleton in order to stretch it out during the moult.

Different crustacean body parts grow according to relative rates which remain proportional to each other throughout the life span unless a major physiological or morphological modification takes place:

$$1/L \cdot dL/dt = k \cdot 1/\lambda \cdot d\lambda/dt \qquad (1)$$

or in an equivalent integrated form:

$$\mathrm{Log}\ L = \mathrm{Log}\ a + b\ \mathrm{Log}\ \lambda \qquad (2)$$

$$\text{and } L = a\lambda^{b} \qquad (3)$$

where L and λ are the lengths of the body parts.

Form (2) of the relative growth equation (also called allometric equation) is usually preferred because it is linear and because there is homoscedasticity of the variances along L and λ (the variances around the mean remain the same for all L's and λ's given λ or L respectively, in the direction of both axes). Since individual variability occurs both for L and λ, there is no independent variable and functional regressions are preferable to predictive regressions for modelling the relationship between L and λ. Use of a principal components analysis to relate size of body parts to orthogonal principal components representing growth factors, avoids the drawback of analyzing successive pairs of intercorrelated variables (Conan and Comeau 1986).

Analysis of relative growth reveals changes in physiology or morphology related to modifications of behavior as a function of age. Changes in relative growth at onset of maturity have been reported for Nephrops (Morizur 1979) and for certain crabs (Vernet-Cornubert 1958) but such changes are highly controversial for other species [e.g., Homarus (Conan et al. 1985)].

Growth in majid crabs

There is no reason to believe that majid crabs differ from other species of crabs for general growth features such as size increment at moult vs age or size, seasonal synchronization of moulting, or synchronization over short periods. There is one major unique feature in that it is generally believed that female majid crabs stop moulting when they reach maturity. This "terminal moult" is accompanied by a change in the shape (morphometry) of the abdomen, which is broadened in order to hold eggs.

Many authors since Tessier (1933) have noted that male majids also undergo a terminal moult to maturity, but this remained controversial for C. opilio until recently (Conan and Comeau 1986, Conan et al. 1985). The terminal moult of males is characterized by a differentiation of the claw which can be quantified as a change in the allometric relationship between measurements of carapace and claw sizes. The terminal moult can occur over a wide range of CW size for C. opilio: three-fold, from 45 to 140 mm CW .

The terminal moult is followed by physiological changes such as degeneration of the "Y" organ, which is believed to control the synthesis of the moult hormone, and by a loss of ability to regenerate missing limbs (G. Vernet-Cornubert, Laboratoire de Physiologie des crustacés, Université des Sciences et des Techniques du Languedoc, Place E. Bataillon, 34060, Montpellier, France, pers. comm.). No crustecdysone is reportedly detectable in "blood" (haemolymph) after the terminal moult (Cormier 1986).

The terminal moult is generally assumed to coincide with onset of functional maturity, i.e., males would become mature by shape (morphometrically) during the terminal moult. They would mate efficiently only after this moult has occurred.

Growth in the genus Chionoecetes

It is generally agreed that females do not moult after onset of maturity. The justification given is that females spawn immediately after hatching of their last brood. The few reports of females moulting or about to moult, although they were carrying eggs, are difficult to ascertain because in all such cases, moult stages were not accurately read. We consider them to be abnormalities which are possible in a few individuals in a population, and should not be taken as the rule.

Male Chionoecetes were previously thought to continue growing after achieving functional maturity while we suggest that Gulf of St. Lawrence C. opilio stop growing. Proponents (Yoshida 1941; Ito 1970; Kon 1980; Tester and Carey 1986) of the former interpretation mention that there are distinct modes in the size frequency distributions of adult males, that males are much larger than females because they keep on growing, that the size difference between males and females is due to the greater energy requirements of the latter for reproduction, and that very large males with clean carapaces (i.e., new moults) are quite common.

Proponents (Conan and Comeau 1986; Moriyasu et al. 1987) of the latter interpretation of the male life cycle report that while premoult immatures are quite common, no premoult, morphometrically mature males are ever found in the catch; that morphometrically mature males never moult in the aquarium while immatures do moult; that morphometrically mature males do not regenerate limbs while immatures do; that the "Y" organ tends to disappear in morphometrically mature males; that the level of crustecdysone is low in morphometrically mature males (Cormier 1986); and that the relative cleanliness of the shell of the males is simply explained by the fact that males can reach the top of their carapace with their claws, while the shorter claws of the females do not allow them to remove epibionts such as sea anemones from the top of their carapaces (Conan, pers. obs.).

Growth in Chionoecetes opilio in the Gulf of St. Lawrence

We believe that both males and females reach a terminal moult at onset of morphometric maturity. The differentiation of the claw is easily identifiable in males by bivariate discriminant analysis of claw size vs carapace size. This differentiation is justified biologically by the fact that morphometrically mature males "grab" females and hold them by their pereiopods in a characteristic way at the end of one of their claws. The grasp is so strong that "grasping marks" are inflicted on the pereiopods which remain permanently apparent. Males with females will use their free claw to fend off bachelor males approaching to take away their mate.

Moulting seasons

There are two distinct moulting seasons for two different groups of crabs:

1) Primiparous females (females which mate and spawn for the first time) moult in early February, and moulting seems particularly synchronized. During this moult their abdomen differentiates from the immature form to the wider mature form which can hold a brood. This moult in February is the terminal moult to morphometric and functional maturity for the females.

2) Non-terminal moults of males and females, and the terminal moults of males, occur from March to late April.

The first moulting season was observed in aquaria by Watson (1970, 1972) during three consecutive years. It was also observed by the authors in 1987 and 1988. Similar observations were made by Carlisle (1957) on Maia squinado. The synchrony of moulting of primiparous females may be a protection against predation (Carlisle 1957), but we believe that it is related to the reproductive strategy of the species.

The second moulting season was identified by observations of both juvenile moult stages in the wild and in aquaria experiments (unpub. data). Juveniles collected in August are all in late postmoult (C1-C3) or intermoult (C4) stages. Postmoult crabs (moult stages B-C2), or "whites", have a low "meat" content and appear in the commercial catch between May and August (Watson 1969). Mallet and Moriyasu (unpub. data) observed that the feeding activity of males, and therefore their catchability by traps, increases during the late postmoult stages (C1-C2).

Increment in size at moult

Limited knowledge is available about snow crab growth at moult. Kon et al. (1968) and Ito (1970) estimated growth at moult of *C. opilio* mainly on the basis of size frequency distribution analysis without differentiating individuals in terminal moult. They assumed that all males kept on growing regardless of their state of morphometric maturity. Early information by Miller and Watson (1976) assumed that maturity of gonads and morphometric differentiation to maturity occured simultaneously and that males did not undergo a terminal moult. Our data show that male gonadal maturity can occur at sizes much smaller than that when the terminal moult and morphometric maturity can occur (Conan and Comeau 1986). The available data on growth at moult of individuals tagged and recaptured in the wild cannot be used to resolve this issue because prior to the knowledge of the existence of a terminal moult, most of the tags were placed on terminal moult individuals which never grew. At this time, we must therefore rely almost exclusively on aquaria observations for quantifying growth at moult despite the fact that growth at moult in aquaria may differ widely from growth in the wild, as shown for other species of crustaceans (Conan 1978).

Aquaria observations (Moriyasu et al. 1987) showed that the relationship between postmoult and premoult size can be modelled satisfactorily by a linear regression. Predictive linear regressions, compared by analysis of variance, show that the growth at moult of males and females does not differ significantly between moults prior to the terminal moult but that it does at the terminal moult. Data are limited, however, for growth at moult of individuals larger than the minimum legal size (95 mm CW). Significant differences, before the terminal moult, were not found for growth at moult prior to and after onset of maturity of the gonads.

Frequency of moulting.

There is no information on the frequency of moulting as a function of age or size, i.e. on the proportion of males or females moulting during a moult season or on the proportion of males and females reaching a terminal moult in any given year. Such information could only be obtained by tagging and recapture experiments of non-terminal moult individuals in the wild. Year-round thermo-regulated aquaria systems are not available to simulate the natural environment for providing reliable information on the natural frequency of moulting.

Relative growth and allometry

Traditional morphometric analyses (Watson 1970; Brown and Powell 1972; Somerton 1980) in male and female *C. opilio* usually refer to the relationships between carapace size and claw size and between carapace size and abdomen width. Conan and Comeau (1986) have suggested that the claw of the male differentiates in order to hold the female during precopulatory embrace. The abdomen of the female differentiates at onset of maturity in order to accommodate its first brood.

Our observations in males smaller than 60 mm CW show that gonads are mature in crabs at about 34 mm CW. This is accompanied by a slight but significant change in morphometry (Comeau 1987). The allometric relationship between carapace width and claw height changes at this size and a change in slope can be detected on a log-log plot (Fig. 1a). Similar changes have been reported in other species of crab. In other majid crabs, this point is referred to as the prepuberal moult, and it was previously assumed that gonad maturity occured after this prepuberal moult.

A second morphometric differentiation occurs when males reach the terminal moult. Proportionally, the claw size relative to carapace width increases much more than during previous moults. On a log-log plot, the allometric relationship between caparace size and claw size is shifted in elevation, but retains its previous slope (Fig. 1b). Conan and Comeau (1986) have designed a method based on a discriminant analysis of the carapace width claw size relationship for identifying preterminal moult from terminal moult individuals (Fig. 2). This moult is homologous to the puberal moult described in other genera of majid crabs.

In the earlier literature, there is a confusion between prepuberal moult, puberal moult, terminal moult, and the occurrence of gonad maturity. For males, the size at 50% gonad maturity (34 mm CW) is much smaller (Comeau 1987) than previously reported by Kon and Honma (1970) or Watson (1970). It was previously believed that morphometric differentiation and gonadal maturity were reached simultaneously and that the males would keep on growing after morphometric differentiation. We have shown that the prepuberal moult of males corresponds to gonadal maturity while morphometric maturity is reached at the terminal moult.

The prepuberal moult and terminal moult are also found in females, but gonadal maturity occurs shortly before the terminal moult rather than at the prepuberal moult (Kon 1980). A slight differentiation of the claw at onset of ther terminal moult is observed in females, as well as differentiation of the abdomen.

We prefer to avoid the word "prepuberal" moult since it erroneously refers to both the gonad and morphometric maturity. We refer to "juvenile" moult to define the angular point in the allometric relationship between claw or abdomen size vs body size (formerly the "prepuberal" moult). We refer to "moult of morphometric maturity" to identify the change in elevation in the same allometric relationship. We have shown that for both male and female *C. opilio*, the moult of morphometric maturity is the "terminal moult". We refer to the individuals as "immature" before the juvenile moult, "juvenile" between the juvenile moult and the moult of morphometric maturity, and "morphometrically mature" after the morphometric maturity moult . In the Gulf of St. Lawrence at least, morphometrically mature *C. opilio* are terminal moult individuals.

Growth curve

The presence of a terminal moult considerably complicates the modelling of an average growth curve for snow crabs. The probability of reaching the terminal moult as a function of size and age should be incorporated in a model. Analytically, this can easily be achieved, however, data is still limited. The proportion of mature and immature individuals observed in a size class should not be used for calculating the annual proportion which reached a terminal moult because this proportion varies (Figs. 3a, b). Virgin populations have proportionally few, large, preterminal moult crabs (Fig. 3a) while in depleted (harvested) populations, the proportion of large, preterminal moult crabs may be as high as 70% (Fig 3b).

Information on both the frequency of moulting of preterminal moult crabs and growth at moult in the wild is not available. Such information will be available only after extensive tagging and recapture of preterminal moult crabs. Tagging and recapture will also provide information on the probability of occurrence of terminal moult crabs as a function of size.

Early estimation of growth curves of commercial-size crabs devoloped after following modes in the size frequency distributions are now not relevant because the existence of a terminal moult was not taken into account. Growth curves of immature and juvenile crabs were fitted on the basis of an analysis of size frequency distributions obtained by a beam trawl around Cape Breton (D. Robichaud; DFO St. Andrews, New Brunswick, pers. comm.). The data required for analyzing growth of recruits is now becoming available, but it currently is still insufficient to build a general growth model. Data on growth at moult of terminal vs non terminal moulters, the frequency of moulting, and the probability of reaching the terminal moult at age or size is required.

Maturity

Reaching a terminal moult has a direct influence on the mating ability of snow crabs. Our observations show that mature male snow crabs carry spermatophores in their vasa deferentia all year round but the abundance of spermatophores may vary between individuals. The maturity indices according to morphological characteristics of the male reproductive organs used by Watson (1970) are subjective. In harvested stocks, such indices or gonadal weight tends to be negatively correlated with body size (Fig. 4). Conan and Comeau (1986) stated that the presence of spermatophores may not necessarily imply that a male is functionally able to mate. The importance of the differentiation of the claw of the male in the act of mating is presently being studied. The term "gonad maturity" should be separated from morphometric maturity (differentiation of secondary sexual characters) and from functional maturity, i.e. ability to mate successfully.

Female gonad maturity is achieved slightly prior to the terminal moult. Morphometric maturity mainly consists of a differentiation of the abdomen to hold the brood and in a slight differentiation of the claw. Functional maturity is reached during the terminal moult.

The size at first maturity, defined as the size at which 50% of the individuals in a population are mature, has little use in the context of a terminal moult. Since animals stop growing at their terminal moult over a very wide range of sizes and disappear from that size class only by dying, the onset of maturity as a function of size or age can only be obtained by following each individual independently, and not by comparing the proportions of gonadally mature and immature crabs in a sample.

We shall now review the existing data on maturity in C. opilio, compare it with information on other species of Chionoecetes, and provide an interpretation for maturity of males and females in snow crab populations.

1. Males: Conan and Comeau (1986) reported that all males larger than 60 mm CW in Bonne Bay, Newfoundland, bore spermatophores in their vasa deferentia. Watson (1970) reports that 50% of the males were mature at 57 mm, but he does not clearly differentiate between maturity of the gonads and morphometric maturity. Our recent observations (unpub. data) indicate that gonad maturity is usually reached in the Gulf of St Lawrence at sizes smaller than 57 mm CW.

   Morphometric maturity was observed by Conan and Comeau (1986) in crabs ranging from 60 to 120 mm CW. Our recent observations (unpub. data) in the Gulf of St Lawrence extend this range from 45-140 mm. The relative abundance of morphometrically immature to morphometrically mature crabs is highly variable from year to year, between geographic locations, and as a function of crab size. It is not known whether a whole age group reaches maturity the same year or over a series of successive years. It is not known what determines the age at which an individual will initiate its terminal moult. We suspect that population regulation mechanisms may control the relative proportion of morphometrically immature to mature animals.

   The sizes at which functional maturity may be reached and its relationship to gonadal and morphometric maturity are controversial. Our aquaria observations (unpub. data) reveal that within a sample of 181 hardshelled mature individuals, 96 immature males ranging in size from 45 to 124 mm CW, and 107 multiparous females ranging in size from 45 to 79 mm CW, no morphometrically immature males mated successfully. Most successful matings involved morphometrically mature males larger than about 90 mm CW. The data from field observations of mating pairs by Taylor et al. (1985) and Conan and Comeau (1986) corroborate aquaria observations.

   We have never found juvenile males (morphometrically immature) mating successfully in the wild. Extensive aquaria observations are presently being conducted in order to determine if juvenile males can successfully mate. Provisional results show that morphometrically mature males are dominant. Juvenile males may mate very briefly with soft shell females shortly after these have reached the terminal moult. This type of mating is totally different from the mating of morphometrically mature males. We do not know yet the importance of this in nature.

2. Females: There is no published information on the incidence of gonad maturity at size for female C. opilio. A mature gonad prior to spawning has a bright orange colour while spent gonads are white. Donaldson et al. (1980) reported that in C. bairdi, 50% of 50 mm CW females have orange ovaries. According to Kon (1980) and Donaldson et al. (1980), it takes about one year from the first appearance of orange ova to achieve functional maturity.

Functional maturity is reached at the same time as morphometric maturity. After the terminal moult, the new shell bears an enlarged abdomen with setae onto which the eggs will be attached and slightly differentiated claws.

Watson (1970) reported that, on the basis of statistics on the morphometry of the abdomen, 50% of female C. opilio were mature at 50 mm CW. The presence of a terminal moult that may be reached over a wide range of sizes from year to year precludes the usefulness of the concept of size at first maturity defined as the size at which 50% of females become mature. Our results (unpub. data) show that, in the southern Gulf of St Lawrence, immature females can reach a size of 70 mm CW while mature females range in size from 44 to 88 mm CW.

Mating

Two types of mating patterns have been observed for C. opilio: 1) terminal-moult males with a hard shell and terminal moult females which have previously spawned and display old grasping marks (multiparous females); and 2) males with soft shell females which have recently moulted to maturity and which are spawning for the first time (primiparous females). The first type of mating occurs from April to May (Taylor et al. 1985; Conan and Comeau 1986; Hooper 1986; Moriyasu et al. 1987). The mating season for primiparous females has never been observed in the wild because of our inability to conduct surveys early in the season due to the presence of thick pack sea ice. Watson (1970, 1972) and Moriyasu et al. (1987) suggest, on the basis of aquaria experiments, that mating with primiparous females occurs in early February while the new shell is still soft; i.e. shortly after the females moult. Spawning (egg extrusion) occurs shortly after moulting. This type of mating was first observed by Watson (1972). It has been assumed that females mate only once and store spermatophores in their spermathecae to ensure successful fertilization of their ova over several years and spawnings.

Taylor et al. (1985) and Conan and Comeau (1986) reported that, in the wild, mating between morphometrically mature males and morphometrically mature hard shell females can occur shortly after the females released their previous brood. Conan and Comeau (1986) suggested that storage of spermatophores in spermathecae was a safeguard mechanism against unsuccessful mating rather than adaptation to a single mating in their lifespan. Our recent observations (unpub. data) tend to confirm that females will normally mate as soon as their previous batch of eggs hatches.

We frequently observed females mating shortly after the terminal moult in aquaria. We are presently investigating the incidence of successful mating of juvenile males with primiparous females. During the mating season of multiparous females, we observed an intense competition and aggression between males both in aquaria and in the wild. It appears that the size of the male is an important factor affecting mating success. Although there was no significant correlation between the size of the male and the size of the female in successful matings (Conan and Moriyasu, unpub. data), males almost exclusively mate with multiparous females which are much smaller than themselves.

Watson (1972) observed mating behavior involving primiparous females in aquaria. He observed small males (71.1 to 98.2 mm CW) mating successfully with females of smaller size. Donaldson and Adams (1986) report that post-moult primiparous females are flaccid, incapable of evasion, and will mate with males 25 to 30 mm smaller in carapace width.

Similar behavior has been observed by us with C. opilio in aquaria but never in the wild (unpub. data). In aquaria, juvenile and morphometrically mature males will mate with soft shell females which recently had a terminal moult. The smallest sizes of juvenile and morphometrically mature males which successfully mated with post-moult females were 47 and 60 mm CW, respectively. The duration of copulatory embrace was observed to be much shorter and the copulatory behavior of males was less competitive than in the case of mating between morphometrically mature males and multiparous females. The prerequisite condition that the male must have a larger carapace size than the female for a successful mating appeared to be less of a deterrent when the mating involved a soft shell (primiparous) female than with hard shell multiparous females. The significance of such matings in reproduction remains questionable since such matings have never been observed in nature in the Gulf of St. Lawrence and since primiparous females represent only about 2% of the stock of egg bearing females in the southwestern Gulf of St. Lawrence.

DISCUSSION

The peculiar growth characteristics of C. opilio have important implications for fishery management. The presence of a terminal moult reached by males over a wide range of carapace size leads to reconsideration of the benefits of setting a minimum harvestable legal size (presently 95 mm CW). In terms of yield-per-recruit, a large proportion of individuals will never grow to legal size and become harvestable. Due to the particular morphometric configuration of juvenile vs morphometrically mature, terminal moult individuals, if the minimum harvestable size were defined as chela size rather than the present carapace width, more terminal moult crabs and less preterminal moult crabs would be harvested (Fig. 5). This would improve the yield-per-recruit by delaying the capture of individuals still growing while allowing the catch of terminal moult individuals smaller than the present minimal legal size based on carapace width.

It appears that initially, the proportion of preterminal moult males in the harvestable size range was probably small and that the fishery has largely harvested old individuals which had accumulated over many years. In heavily exploited locations, a change in the relative proportions of preterminal moult, young terminal moult, and old terminal moult crabs has been observed. Proportionally, more crabs in heavily harvested stocks are preterminal moult crabs and subsequently, a higher percentage of "white" and "pink" postmoult crabs are present in the catch. The "pinks" and "whites" have low flesh content ("meat yield") and are of lower commercial quality.

The peculiar maturity and mating patterns observed for snow crabs may have an important influence on recruitment. It was previously believed that all snow crabs were functionally mature before reaching the minimal legally harvestable size and that they were able to mate with several females. Our recent observations suggest that in nature, mating occurs mostly, if not exclusively, between terminal moult males and terminal moult females. The incidence of recently moulted, primiparous females appears to be low in the populations monitored. We never observed pairing in the wild, between nonterminal moult males and females. In most of the couples observed, the males were larger than the present 95 mm minimal harvestable size.

The effect of heavy exploitation of males larger than 95 mm CW on stock reproductive potential is not yet fully understood. If morphometrically mature males smaller than 95 mm CW can now mate because of reduced competition resulting from depletion by fishing of large dominant terminal moult males, the consequences of possible genetic selection for smaller crabs should be considered. Small, non-commercial individuals may now be selected if the size at terminal moult is genetically determined. On the other hand, if males smaller than 95 mm CW do not mate efficiently, the storage of spermatophores from large males by females may partially compensate for the depletion of large terminal moult males by fishing.

Since moulting occurs in the spring and crabs take several months to fill up their new carapace with flesh, it does not seem appropriate to reopen the fishery in the fall after it has been closed because of an over-abundance of "whites" in summer. Whether the fishing season is set in the spring or in the fall, a high fishing level year after year leads to the relative depletion of older terminal moult crabs, which have accumulated on the fishing ground over several years. If fishing effort becomes sufficiently intense, only recent recruits in "white" condition would become available during the spring fishing season. A rotation of fishing grounds from year to year would minimize the problem of over-abundance of low-quality white crabs in the catch while maintaining an acceptable catch rate of hard crabs.

A detailed knowledge of growth, including the probability for crabs to reach a terminal moult as a function of size or age, is required prior to developing an accurate yield-per-recruit model. Such a model would allow definition of a minimal claw size, an optimal effort, an optimal catch/biomass ratio, and an optimal rotation period for fishing grounds if recruitment was assumed to remain stable.

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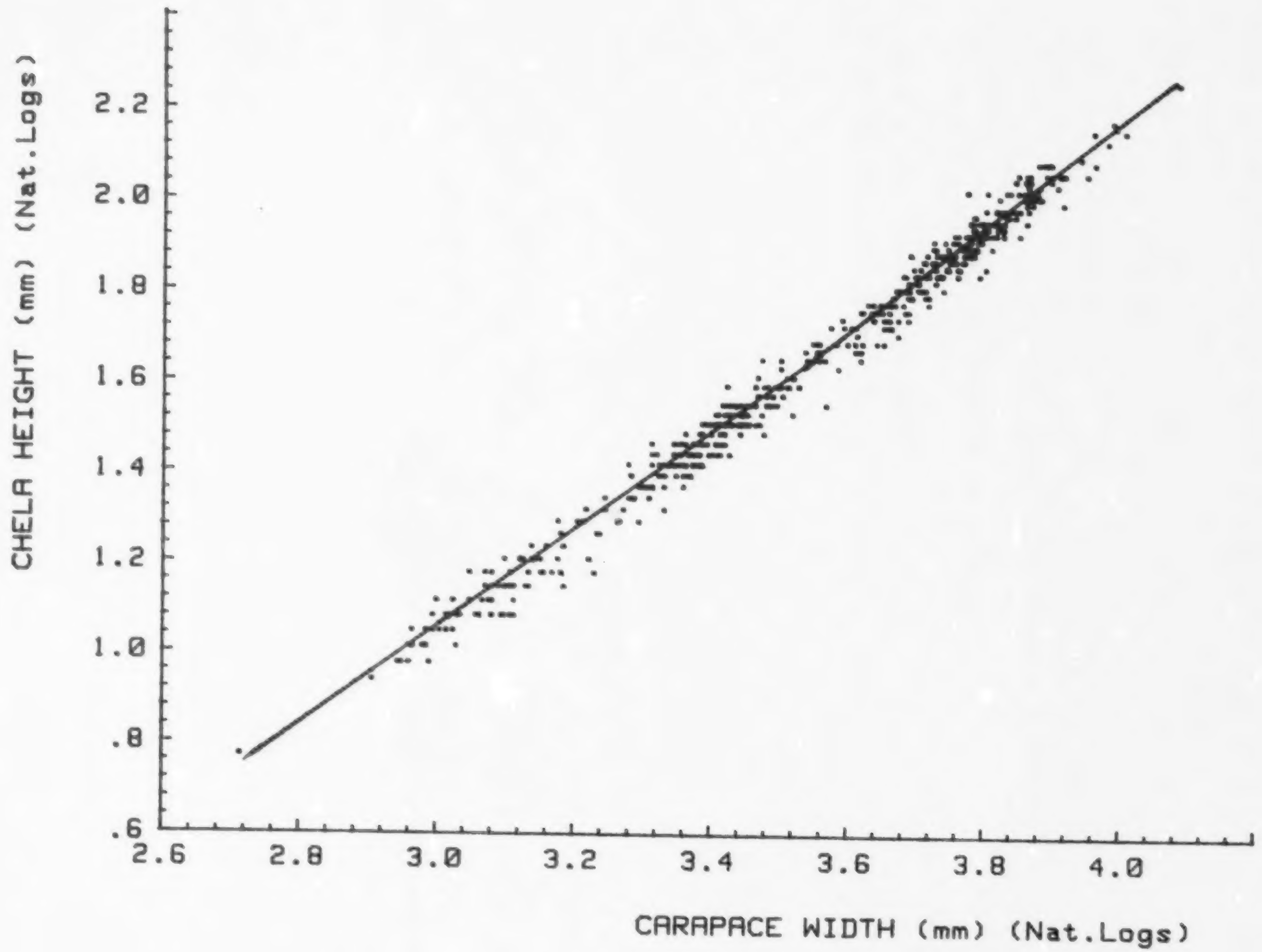

Figure 1a. Allometric relationship (logarithmic scale) between chela height and carapace width from male snow crabs smaller than 60 mm CW from Bonne Bay (N= 270, modified from Comeau 1987).

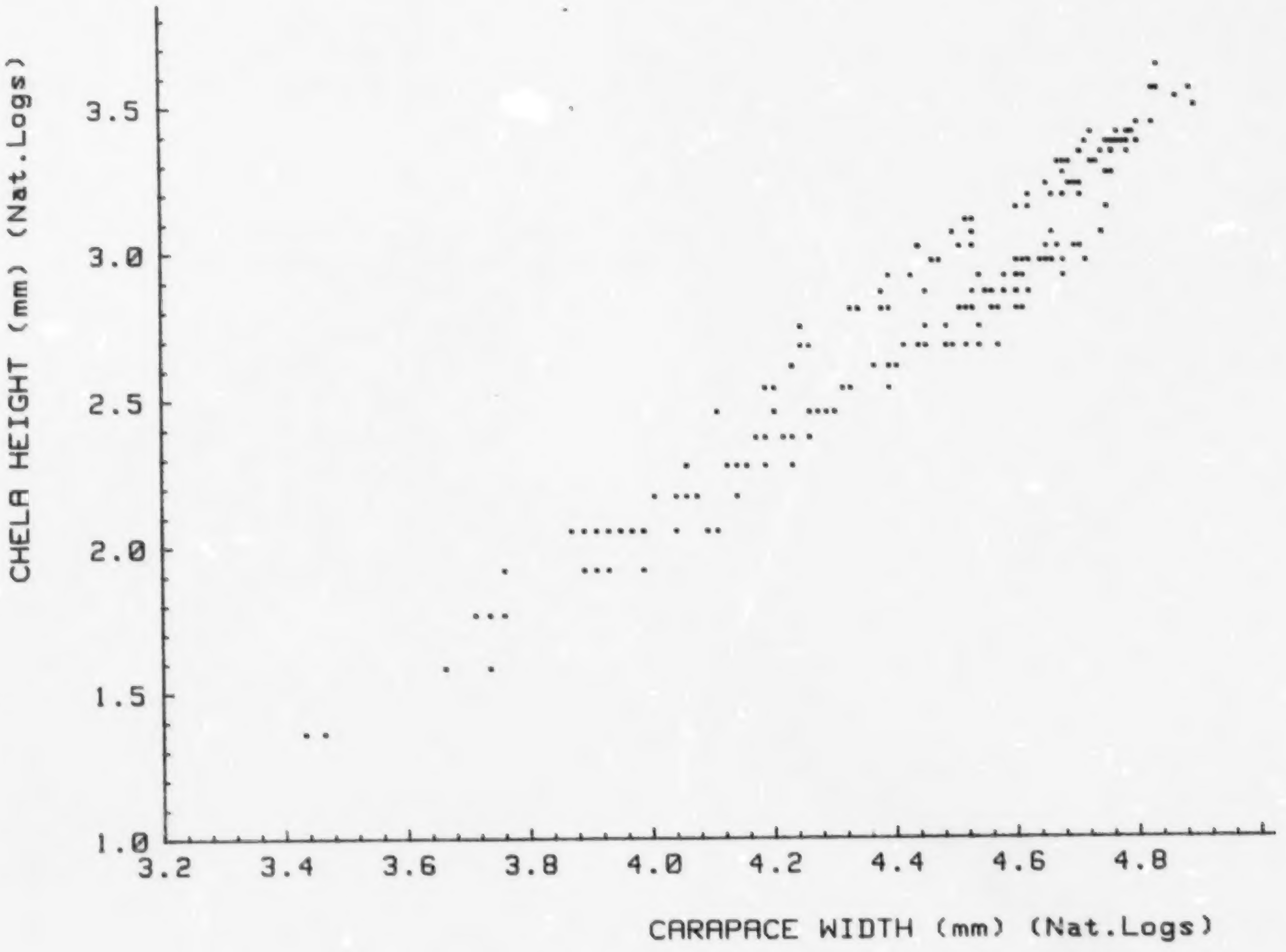

Figure 1b. Allometric relationship (logarithmic scale) between chela height and carapace width from male snow crabs from Baie des Chaleurs (N= 217, after Conan and Comeau 1986).

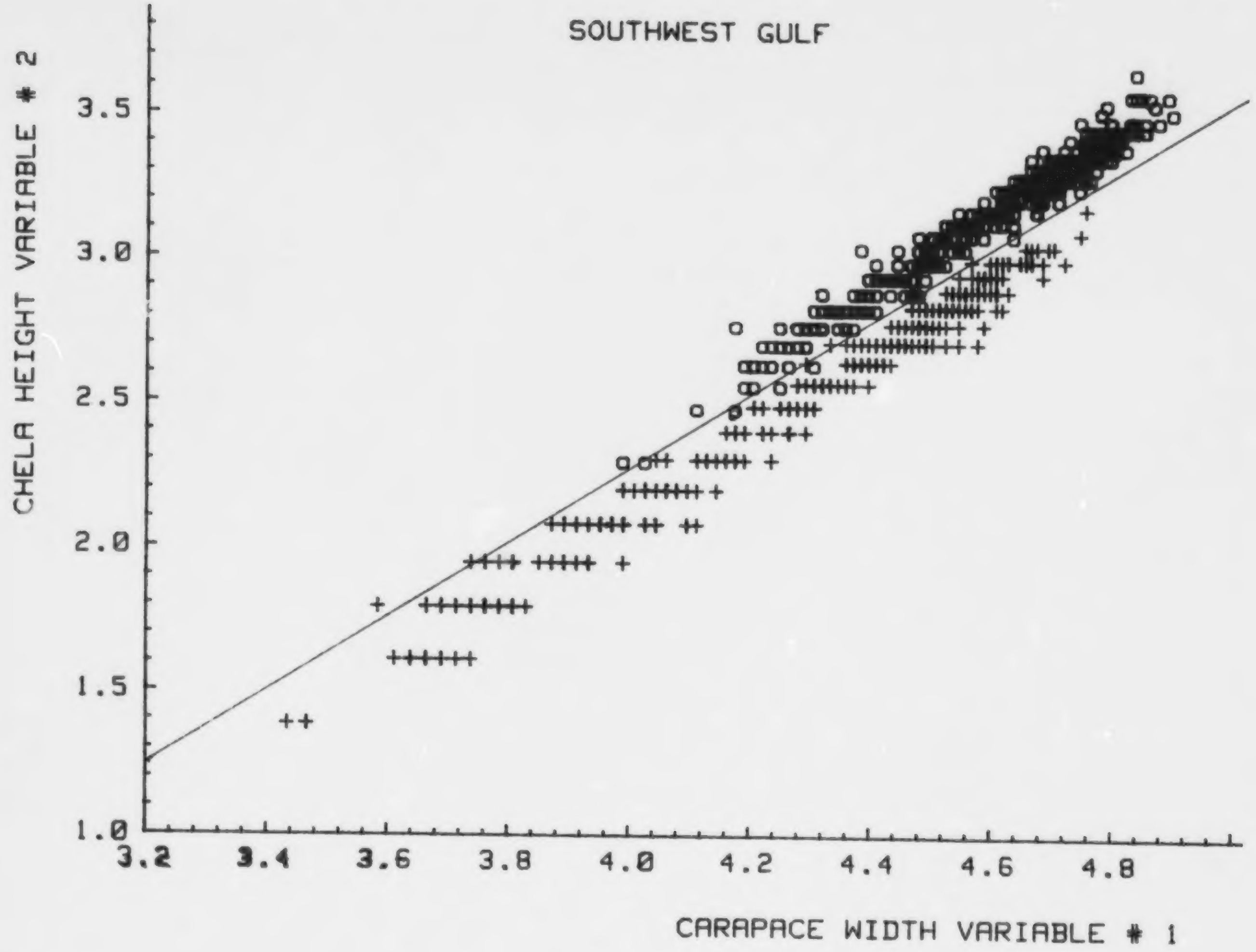

Figure 2. Discriminant analysis of observations from southwest Gulf of St. Lawrence with the representation of the cutting line separating the two swarms of points. The discrimination is about 100% efficient (0= mature males, += immature males), N= 784 (after Conan and Comeau 1986).

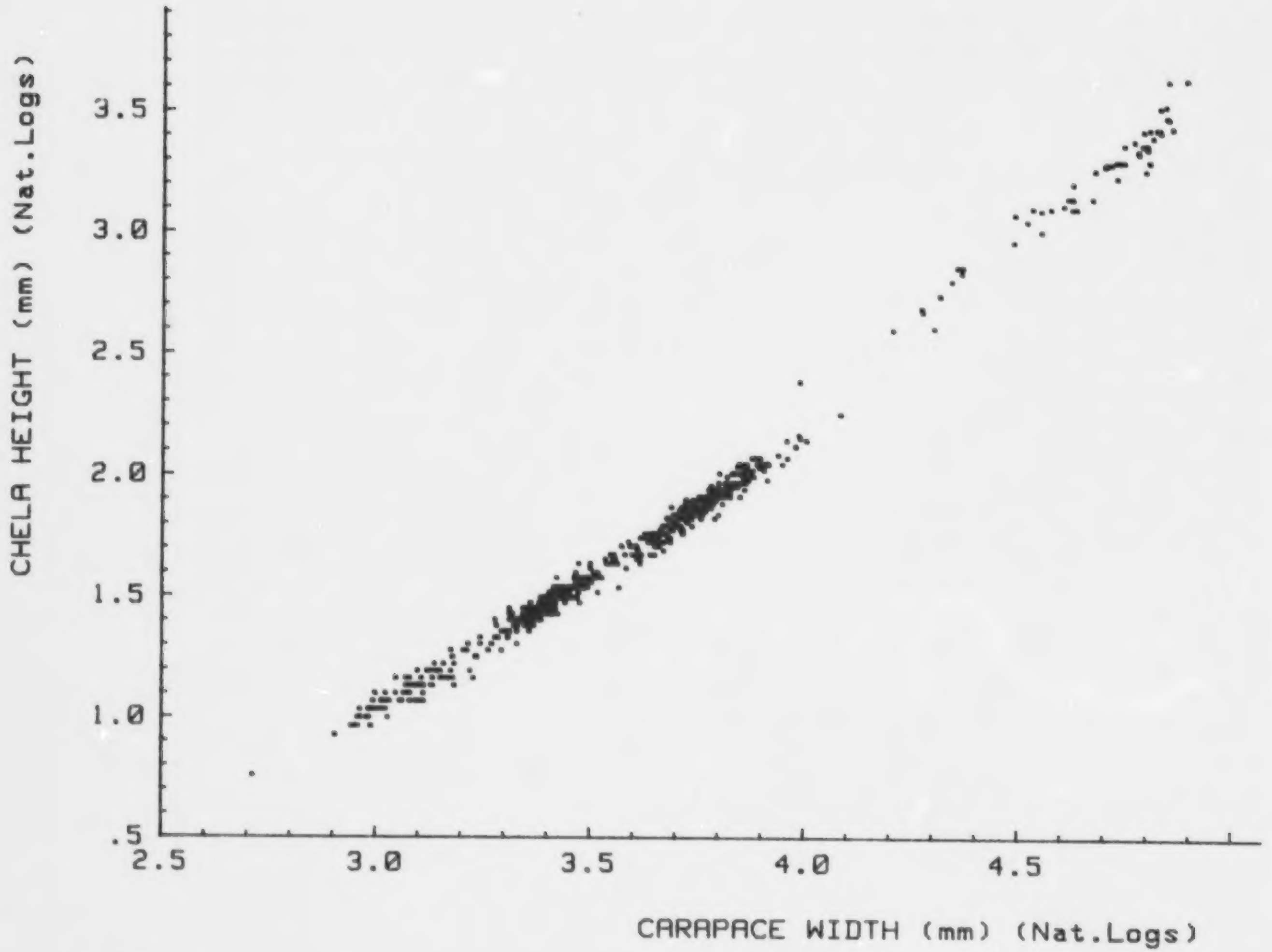

Figure 3a. Allometric relationship (logarithmic scale) between chela height and carapace width from male snow crabs from a non-exploited stock in Bonne Bay (N= 270, modified from Comeau 1987).

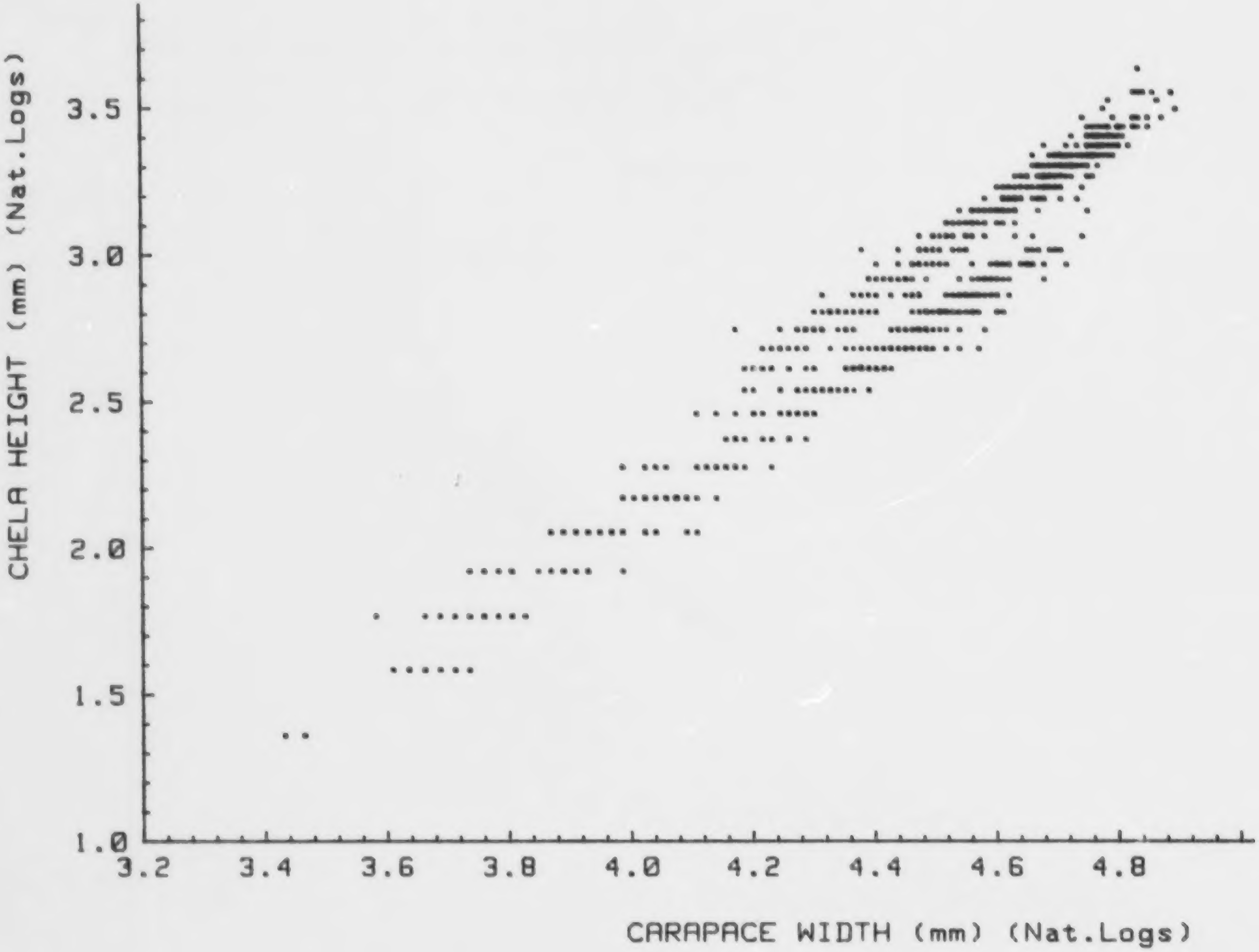

Figure 3b. Allometric relationship (logarithmic scale) between chela height and carapace width from male snow crabs from an exploited stock in the southwest Gulf of St. Lawrence (N= 784, modified from Conan and Comeau 1986).

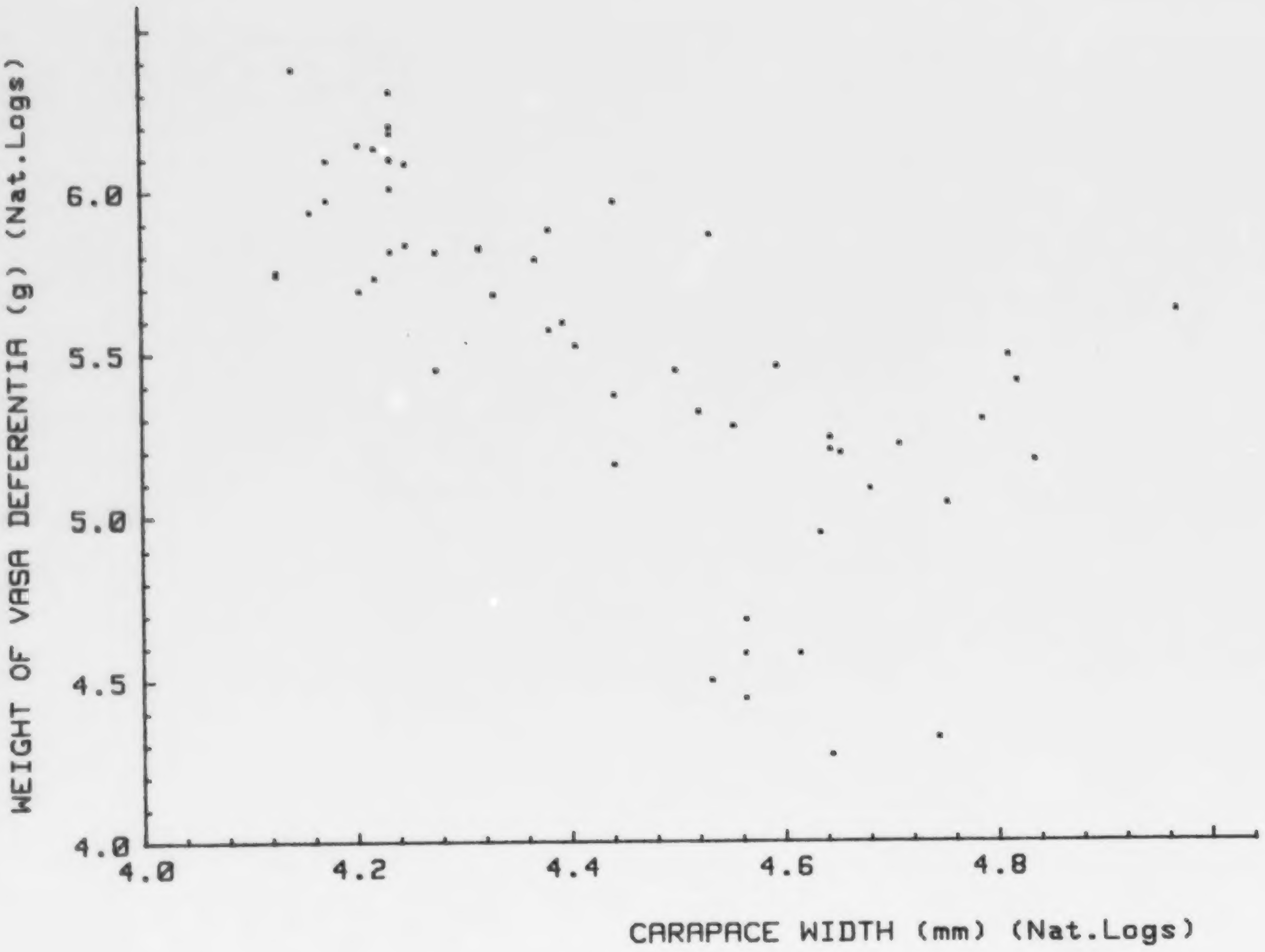

Figure 4. Relationship (logarithmic scale) between wet weight of the vasa deferentia and carapace width from male snow crabs collected in Baie des Chaleurs (coefficient of correlation = -.69, N= 66).

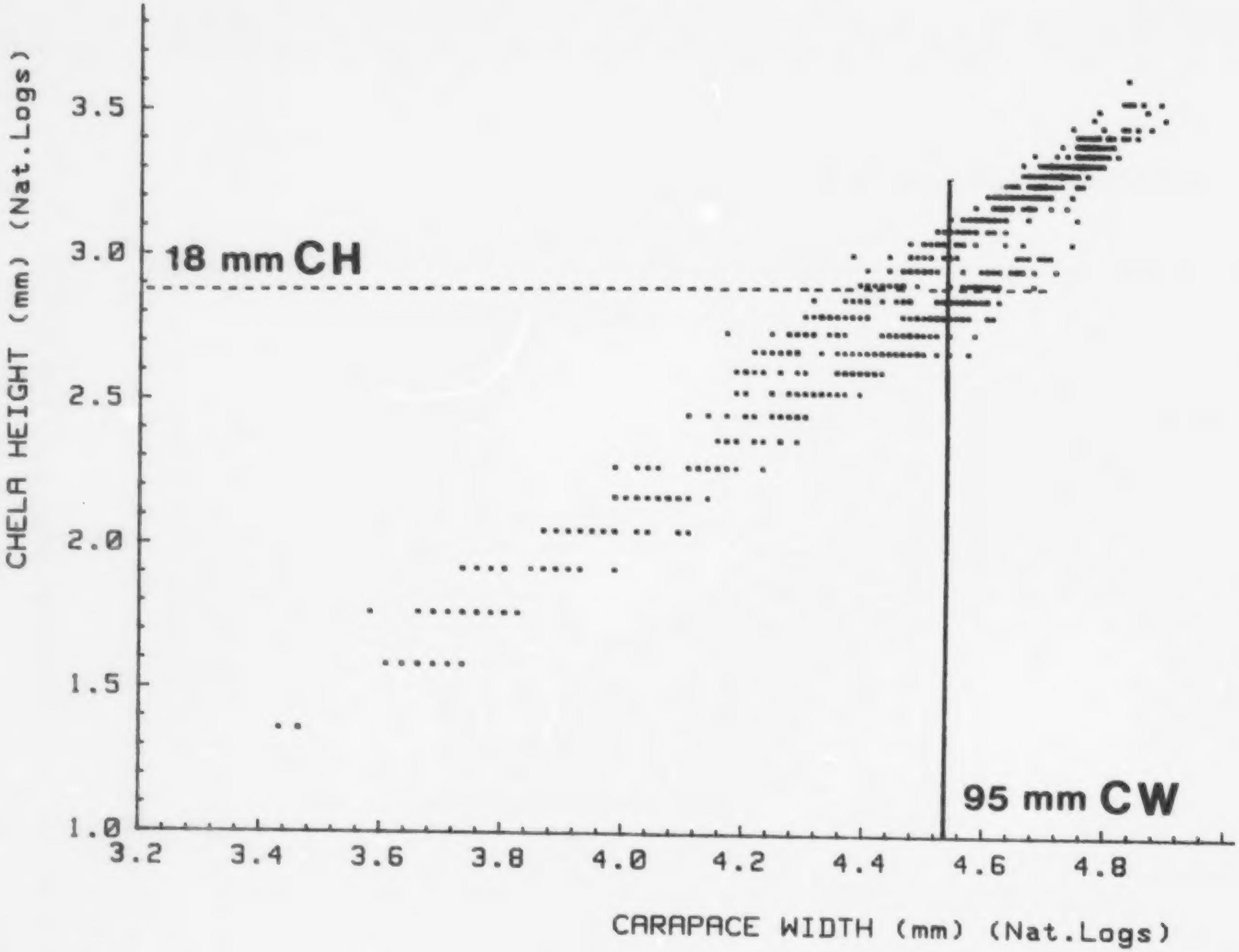

Figure 5. Allometric relationship (logarithmic scale) between chela height and carapace width from male snow crabs from the southwest Gulf of St. Lawrence (N= 784, modified from Conan and Comeau 1986).

C. A Review of the Literature
Pertaining to the Reproductive Biology of the Genus *Chionoecetes*
by D.M. Taylor

INTRODUCTION

While the relationship between fecundity levels in commercially important decapod crustacean populations and subsequent levels of recruitment into the fishery is not clear, implicit in responsible management strategies is the goal of assuring optimum egg production. Two *Chionoecetes* species, *C. opilio* and *C. bairdi*, support substantial commercial fisheries, and since only large males are exploited, it has until recently been assumed that the reproductive capacity of the stocks has been maintained at optimal levels.

While fisheries regulations in Alaska prohibit the retention of female *Chionoecetes* and the Canadian minimum size of 95 mm (CW) effectively excludes female *C. opilio* from commercial landings (Miller 1976), the effects of factors such as male parent size, temperature, reproductive stage of females, and other biological and environmental factors may have an impact on *Chionoecetes* population fecundity.

Elner and Robichaud (1983) have provided the most recent "review" of published research on *Chionoecetes* reproduction. While this review is fairly complete, covering most pertinent literature up to the time of publication, recent advances in our knowledge of *Chionoecetes* breeding biology require that an additional comparative review of published research on reproduction in *Chionoecetes* be undertaken. In addition, some results of unpublished data from field and laboratory investigations conducted on Newfoundland *Chionoecetes opilio* are included here.

FEMALE MATURITY

Generally, maturity in female *Chionoecetes* has been based on morphometrics (relationship between carapace width (CW) and the width of the fifth abdominal segment), ovary condition, and the presence of extruded eggs. Several authors have used the size at which 50% of females in a population are mature as a measure of the populations' maturity. Yoshida (1941) determined the size at 50% maturity for *C. opilio elongatus* as 63 mm (CW). Squires (1965), Watson (1970), and Elner and Robichaud (1983) have stated that the size at 50% maturity for *C. opilio* from Newfoundland and Labrador, the Gulf of St. Lawrence, and Cape Breton Island is 65 mm, 50 mm, and 51 mm (CW), respectively. Donaldson et al. (1981) define size of 50% maturity for *C. bairdi* from Alaska to be 83 mm CW.

However, Somerton (1981) disputes the utility of this measure, preferring the use of the mean size of mature females in a population because "it is independent (except for density dependent effects on growth) of variation in year class strength". He also states size at 50% maturity varies with the natural mortality rate while mean size of mature females does not.

Tester and Carey (1986) use mean size of mature C. tanneri females (102.3 mm CW) as a measure of female maturity in Oregon.

FECUNDITY

Fecundity estimates of Chionoecetes females have been conducted by various researchers. Brunel (1961), Watson (1969), Thompson (1979), Elner and Gass (1984), Elner and Robichaud (1983), Davidson et al. (1985), and Taylor (unpub. data) have estimated fecundity for C. opilio from Atlantic Canada. Haynes et al. (1976) provided comparative estimates of fecundity for C. opilio from the Gulf of St. Lawrence and the Bering Sea. Jewett (1981) has compared fecundity of C. opilio from the Chukchi Sea, Alaska, to the results of Haynes et al. (1976) in an attempt to demonstrate variations in snow crab fecundity because of geographic location.

Fecundity of C. opilio elongatus from Asian waters has been estimated by Ito (1963) and Kanno (1987), and C. bairdi fecundity from Alaska has been reported by Hilsinger (1976), Adams and Paul (1983), and Somerton and Meyers (1983).

Most estimates of fecundity were obtained by drying individual orange, recently-extruded egg masses. Subsamples of the dried eggs were then weighed, counted, and the total weight of the egg mass was divided by the average weight of an individual egg. While several researchers have employed different methodologies (Haynes et al. 1976, for example), the above described methodology is considered the most efficient and accurate alternative to actually counting eggs individually. Elner and Gass (1984) presented a comparison of total fecundity for various C. opilio populations (Table 1).

Chionoecetes females are most active reproductively during the spring. For most species, the time period from April to June encompasses a breeding migration (Taylor et al. 1985; Hooper 1986), larval release (Ito 1963; Kon 1974; Hilsinger 1976; Paul 1984; Taylor et al. 1985; Hooper 1986), mating (Watson 1970, 1972; Takeshita and Matsuura 1980; Adams 1982; Taylor et al. 1985; Hooper 1986) and egg extrusion (Watson 1970, 1972; Takeshita and Matsuura 1980; Adams 1982; Paul 1984; Kanno 1987).

The fact that these events normally occur during the spring is of particular importance for larval survival. Larval release during the spring coincides with yearly plankton blooms which may assure adequate food availability for larval growth and development.

BREEDING HISTORY

Somerton and Meyers (1983) report that egg clutch size of primiparous C. bairdi is approximately 70% that of multiparous females of the same size. This difference is attributed to either the energetic cost of moulting to maturity or to the fact that pre-moult primiparous females have a smaller volume within the body cavity for ovarian tissue.

Separation of primiparous and multiparous females may be achieved by examining the shell condition of the crabs (Somerton and Meyers 1983). Primiparous females' exoskeletons are clean, bright, have few scratches and demonstrate little wear. The exoskeleton of multiparous females is darker, with many scratches and barnacles and other epifauna present. Paul (1984), separates primiparous from multiparous C. bairdi by the absence of male grasping marks on the legs of primiparous females.

The breeding history of female Chionoecetes is an important factor in determining its fertile period. Paul and Adams (1984) demonstrated that while primiparous C. bairdi are fertile from 1-28 days following their moult to maturity, multiparous females, if not mated within 1-7 days, will produce eggs fertilized by stored sperm. Paul (1984) found that 97% of multiparous female C. bairdi produced viable egg clutches using sperm stored for 1 year, while 71% of females held isolated from males produced viable egg clutches from at least 2-year old sperm.

Watson (1970) determined that female C. opilio can produce at least two egg clutches from sperm received during copulation following the moult to maturity. Elner and Gass (1984) found that 87% of the female C. opilio examined from Cape Breton had sufficient sperm stored in the spermathecae to fertilize at least one additional egg clutch. In Bonne Bay, Newfoundland, large numbers of multiparous females have been captured in the spring by trapping. These females almost always had newly extruded orange eggs that had been fertilized by stored sperm (unpub. data). This sampling was coincidental with the deep to shallow water migration, reported by Taylor et al. (1985) and Hooper (1986), after which multiparous females mate with large males. These preliminary data may support the theory of Kanno (1987) that snow crab may have a reproductive cycle of two years.

PARENT SIZE

Female Parent Size

With the exception of Elner and Gass (1984), all investigators of Chionoecetes fecundity have found significant relationships between the number of uneyed eggs carried and carapace width. While there is a wide range in the number of eggs carried within a particular size group of females, fecundity generally increases with carapace width. While Elner and Gass (1984) report no significant relationship between the number of eggs carried by female C. opilio and parent carapace width in their study, it is perhaps noteworthy that the data used were collected in late November, and significant egg loss could have occurred during the earlier months of egg incubation. Elner and Gass (1984) did find a significant correlation between carapace width and the number of eyed eggs carried.

Male Parent Size

Adams (1982) reported that small males had little trouble mating with newly-hardened, primiparous *C. bairdi* but that old-shelled, multiparous females resisted mating attempts by small males. No male under 120 mm CW was able to mate successfully with a multiparous female.

These results for *C. bairdi* are supported by laboratory work conducted by Conan and Comeau (1986) on *C. opilio* from the Gulf of St. Lawrence. While morphometrically mature males were able to successfully mate with multiparous females, morphometrically immature males were apparently intimidated by morphometrically mature males and exhibited avoidance behavior.

Taylor et al. (1985) observed sublegal (<95 mm CW) *C. opilio* males participating in the deep-to-shallow water breeding migration in Bonne Bay, Newfoundland, and their successfully mating with multiparous females. They also found (unpublished data) that not only can morphometrically mature sublegal size males successfully mate with multiparous females but that in the absence of competing larger males, morphometrically immature males can mate with multiparous females, some of which are larger than the males. However, in at least one instance, only one spermatheca of the mated female contained new spermatophores. This supports Adams (1985) theory that female intergonopore distance versus the spread of the male's first pleopods may be an important factor in determining effective mating success of male *Chionoecetes*.

EFFECTS OF LOCATION ON FECUNDITY

Haynes et al. (1976) showed that Atlantic female *C. opilio* have a higher fecundity for a given carapace width (CW) than do females from the Bering Sea. Davidson et al. (1985) demonstrated considerable variation in the mean fecundity of *C. opilio* stocks from four regions of Atlantic Canada.

Jones and Simmons (1983) studied eleven New Zealand populations of the burrowing mud crab *Helice crassa* stretching over 11° of latitude. While crab densities were higher at low latitudes, size at maturity and fecundity increased with latitude. They also noted, however, that the proportion of ovigerous females was not correlated with latitude.

In Newfoundland, comparison of the fecundities of seven discrete snow crab populations resulted in a positive correlation of fecundity with carapace width (unpub. data). While the study was initiated to investigate possible variation in fecundity levels with latitude, no such relationship was found. However, it was noted that three unexploited populations had significantly more eggs per female CW size grouping than did those females sampled from areas where there is an ongoing commercial fishery. There was no correlation between the number of eggs per female size category and the estimated age of sperm in the spermathecae.

FECUNDITY LEVELS VS. INCUBATION TIME

Brunel (1962) and Kon (1974) reported a 50% loss in eggs of C. opilio over the egg incubation period. These findings are supported by Elner and Gass (1984) for C. opilio from Cape Breton Island. Hilsinger (1976) reported similar egg loss in C. bairdi. While the decrease in egg number over time can be attributed to several sources, e.g. death and disintegration of abnormal embryos, loss of unfertilized eggs, or predation/parasitism, the effect on the magnitude of larval hatching cannot be ignored. Egg loss over the incubation period will undoubtedly vary from region to region, and in considering fecundity of various Chionoecetes populations, studies should address this point.

Although more difficult, due to the fact that eggs are more susceptible to handling loss as development progresses, fecundity estimates based on eyed egg numbers may be more realistic than those based on recently extruded orange eggs (Elner and Gass 1984). Also, it has been shown that unfertilized primiparous C. bairdi are capable of producing full clutches of unfertilized eggs that are initially indistinguishable from fertilized eggs carried by primiparous females that have mated successfully (Adams 1982). Counting of only eyed eggs would remove any bias arising from this factor and may provide a more accurate estimate of fecundity levels of populations where parasite predator burdens vary in severity.

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Table 1: Estimates of total fecundity and regression fecundity (y) with carapace width (x) for female snow crabs, *Chionoecetes opilio*. from various areas (modified from Elner and Gass 1984).

Sample area	No. of females sampled	Fecundity regressions	Corr. coef. (r)	Mean fecundity	Range
Newfoundland [a]	51	$Y = 6.4080X^{2.169}$	0.7767	52,048	37,934- 81,239
Anticosti[a]	98	$Y = 13.2530X^{1.9922}$	0.7472	58,760	12,134-122,891
Pleasant Bay [a]	98	$Y = 38.4554X^{1.7649}$	0.6347	74,475	32,564-128,433
Gabarus [a]	115	$Y = 14.7361X^{1.9859}$	0.6598	80,068	42,284-120,378
All four of the above areas[a]	361	$Y = 9.2490X^{2.0893}$	0.7694	66,338	12,134-128,433
Southeastern Bering Sea[b]	42	$Y = 0.4905X^{2.7206}$	0.7329	36,273	- -
Gulf of St. Lawrence[b]	99	$Y = 0.0012X^{4.200}$	0.8086	-	20,000-140,000[c]
NW Cape Breton Island[d] (non-eyed)	25	$Y = 3092.23X^{0.70}$	0.223	61,430	31,276-102,022
NW Cape Breton Island[d] (eyed)	25	$Y = 147.17X^{1.42}$	0.500	58,193	23,144- 85,365
Chukchi Sea[e]	63	$Y = 0.0249X^{3.4822}$	0.767	-	12,900- 37,100

[a] From Davidson (1983)
[b] From Haynes et al. (1976)
[c] From Watson (1969)
[d] From Elner and Gass (1984)
[e] From Jewett (1981)

D. Overview of the Distribution and Movement of Snow Crab (*Chionoecetes opilio*)

by

R. Dufour

INTRODUCTION

The concept of migration has been defined in many ways but has always been based on spatial movements. Migration can be broadly defined as a behaviour specially evolved for the displacement of an animal in space (Dingle 1980). There are two kinds of movements associated with migration of benthic snow crab (*Chionoecetes opilio*): local, short-range movements and large scale movements. Local movements are of a few hours duration, usually repeated on a diurnal basis. Large scale movements, here identified as migrations, are from one distinct geographic location to another, lasting at least a few days and sometimes longer.

Understanding the migration routes of snow crab movement is important for many reasons. At a species level, seasonal migrations not only allow occupation of regions that would be unfavourable in the absence of migration but also enable animals to maintain a higher average density and activity rate (Odum 1971).

For a fishery, knowing the location of populations on a seasonal basis increases the efficiency of the fleet, thus improving income. That knowledge is also essential in the management process when information on quotas and resource allocation is required.

This paper will summarize our understanding of the dynamic movements of snow crabs in Atlantic Canada.

Distribution in relation to temperature, bathymetry and sediment

In Atlantic Canada, commercial snow crab fishing grounds are located in the St. Lawrence Estuary, in the Gulf of St. Lawrence, around Cape Breton Island, and off the east coast of Newfoundland (Fig. 1). Adult snow crabs live most commonly on mud bottoms at temperatures ranging from -0.5 to 5.0°C (Elner 1982). They have been found in temperatures up to 9.7°C (Powles 1966) but are most abundant between -1.5 and 2°C in the Magdalen trough in the southwestern part of the Gulf of St. Lawrence (Powles 1968). These grounds are generally found in the 70-140 m depth range in the Gulf, compared to 45-245 m around Cape Breton and 170-380 m off Newfoundland.

At the beginning of the fishery in the 1960's, Brunel (1960, 1961, 1962) and Powles (1966) observed that snow crabs preferred mud substrates, but occasionally occurred on rock-gravel bottoms. Later, Miller (1975) found aggregations of smaller crabs [< 40 mm carapace width (CW)] on rocky bottoms, and from field observations, postulated that mature females and immatures of both sexes were highly aggregated, whereas large males (>70 mm CW) had a more random distribution. Robichaud (1985) also found an aggregated distributional pattern for mature females and juveniles in the Cape-Breton area.

Several studies (Miller and O'Keefe 1981; Greendale and Bailey 1982; Coulombe et al. 1985) have found that size of males was correlated directly with depth. Other authors, with more data on substrate characteristics, related crab distribution, size, and density to bottom type (Powles 1968; Robichaud 1985). Coulombe et al. (1985), studying Baie des Chaleurs snow crab, found that juveniles (45-55 mm CW) preferred mud-gravel substrates in shallower waters. Adults were found deeper on mud and mud-sand bottoms. They then postulated that juveniles migrate from shallow, heterogenous substrates to deeper, muddier ones on reaching maturity.

Juveniles (37-51 mm CW) may sometimes be absent from apparent "nursery" areas (Robichaud 1985), possibly because of recruitment failure or a previous migration away from the area. Pereyra (1967) suggested similar hypotheses to explain a similar observation with *C. tanneri* off the Oregon coast. Robichaud (1985) found smaller crabs (< 37 mm CW) on a mud bottom with the adults. Brethes et al. (1987) found juveniles (<30 mm CW) over a wide area having specific conditions of depth (>60 m), temperature (<3°C), and substrate (> 40% mud), but highest densities (>4000 km^{-2}) were in intermediate water layers at 80-110 m-depth in the northern Gulf of St. Lawrence.

Bouchard et al. (1986), analysing the size distribution of snow crabs from exploited (1977-82) and unexploited (1980-81) grounds in the southwestern Gulf of St Lawrence, found some evidence supporting the findings of Coulombe et al. (1985) on migration of snow crabs towards deeper water with increasing size. They explained the resilience of the Southwestern Gulf stock to exploitation by adopting Ricker's (1975) concept of "recruitment by platoons". Essentially, they identified two waves of recruitment during the year in the fishery. The first one, formed of prerecruits already on the fishing ground, enter the fishery in spring or early summer when they moult to commercial size. The second wave, composed of prerecruits living in shallower depths, become available in late summer or fall after their migration from shallow, unexploited locations to the deeper fishing grounds, with moulting to commercial size occurring in this time interval.

Local movements

Maynard and Robichaud (1986), after tagging snow crab with ultrasonic tags, recorded the diel movements of five crabs for a maximum time duration of seventeen days (late summer-fall) in the Bay of Islands, Newfoundland. Activity appears to be related to light conditions, as suggested by Brunel (1960, 1961, 1962), with crabs most active at low light levels. The three male and two female crabs had different behaviours during the tracking period, and no clear pattern of diel movement emerged. Random movement of one male (day and night) and one female (day only) crab was reported by Maynard and Webber (1987).

Large scale movements

A number of tagging experiments have been conducted in the Gulf of St Lawrence. The first experiments were carried out by Powles (1968) and Watson (1970), who tagged mainly commercial size males in 1966 and 1969, respectively. Their results suggested that most crabs moved less than 17 km from the release points, although movements up to 50 km after three years occurred. Movement seemed to be random, allowing some mixing of crabs between the offshore grounds and Gaspe coastal areas. Results from a similar tagging experiment of male crab in the same area (Watson and Wells 1972) confirmed the absence of extensive, directed snow crab movement. The majority of recaptures (80-90%) occurred within 25 km of the point of release, although a few crabs moved up to 56 km in less than a year. In the Cape Breton area, 99% of tagged crabs (majority > 95 mm) were recaptured <20 km from their release points up to five years after release (R. Elner and D. Robichaud, Dept. Fish. and Oceans, St. Andrews, N.B., pers. comm.). In Bonavista Bay, Newfoundland, tagging showed average crab movements of 12 km up to six years after release, (D. Taylor, Dept. Fish. Oceans, St. John's, Nfld, pers. comm.). Most movement (77%) observed by Taylor was oriented perpendicular to the bottom slope. In the Kodiak area, Alaska, Colgate (1982) reported on tanner crab (C. tanneri) movement based on six years of recaptures (1973-79). Some crabs ranged widely in particular areas, though average movement during the course of his survey was only 24 km.

From a three-year tagging study in the eastern Bering Sea, McBride (1982) reported extensive movement of C. opilio, averaging about 78 km from the point of release and generally oriented in the south to southwest.

Although many authors support the idea of seasonal snow crab movement, perhaps the most significant study is by Hooper (1986) in Bonne Bay, Newfoundland. In study of an unexploited snow crab population, males and females were found in shallow water, where they were breeding, only in April and May. They apparently moved into deeper (>40 m) water in other months of the year. Maximum pair density (approximately 1 pair m^2) was found among algal covered rocks between 10-40 m. Before mid-May, solitary crabs (as opposed to mating pairs) were rare. Females seemed to occupy a different ecological habitat than did the males when they were not mating. They may also bury in the sediment at other times of the year staying motionless for very extended periods of time. Taylor, et al. (1985) postulated from Hooper's (1986) results that males may migrate in the spring from deep water to shallow water for breeding.

A winter breeding movement is also mentioned for C. tanneri off Oregon (Pereyra 1967). Adams (1979) reports seasonal movement of southeastern Bering Sea snow crab from Slizkin's (1974) study.

DISCUSSION

Snow crabs distribute themselves in their habitat according to environmental factors such as depth, temperature, and substrate type. Juveniles are more commonly encountered on heterogenous (rock-gravel-mud) bottoms at shallower depths, while adults are usually caught on deeper, mud bottoms. Small-sized juveniles (<37 mm CW) have, however, been found with adults in Cape Breton (Robichaud 1985).

Local movements exhibited by snow crabs seem random, and crabs are more active during dark periods of the day and at night. Different short-term behaviour may also characterize male and female crabs, the females possibly burying themselves in the sediment for long periods of time outside the breeding period. Short-term movements made by snow crabs seem to be related primarily to local shelter, food, competitor and predator spatial distributions (Herrnkind 1983).

On a long term basis, few long distance movements were recorded, and an average movement of <25 km in most areas confirms the lack of extensive movements of Atlantic Canada snow crabs. Bays, gullies and other obstacles common in the Gulf region may sometimes affect the direction and distance of movement. The absence of bays and a relatively uniform bathymetry in the eastern Bering Sea may have contributed to the greater average distances travelled in that area. Therefore, apart from the larval dispersal period, contacts between crabs from distant populations in Atlantic Canada are not probable.

Although further investigations are required, two differents kinds of yearly oriented movements seem to occur. The first, a breeding migration, occurs in the spring (April-May) when the males pair with the females and move to shallower grounds for mating. The males may hold a female in the embrace position for up to two months, feeding and protecting her during this time (Hooper 1986). The reasons for this migration into shallower water are still unclear but may be related to environmental and hydrographic factors. The second movement type, which needs to be confirmed and is not yet well understood, is a deep-water movement of juveniles to the mud bottoms preferred by adults (Coulombe et al. 1985). In the Gulf of St. Lawrence, snow crab size is directly related with depth and proportion of fine sediment in the substrate (Miller and O'Keefe 1981; Greendale and Bailey 1982; Coulombe et al. 1985; Bouchard et al. 1986). The recent discovery by Conan and Comeau (1986) of up to 40% preterminal moult males on fishing grounds in the southwestern Gulf of St. Lawrence suggests that this migration may not be totaly explained by the functional sexual maturation of the juveniles. The "recruitment by platoons" suggestion of Bouchard et al. (1986), with two pulses per year to the adult grounds, brings an interesting new perspective of the dynamics of crab movement on the fishing grounds. The fact that juveniles may live in different areas and feed differently than adults (Coulombe et al. 1985; Robichaud 1985; Brethes et al. 1984) may ensure some level of conservation to an exploited stock.

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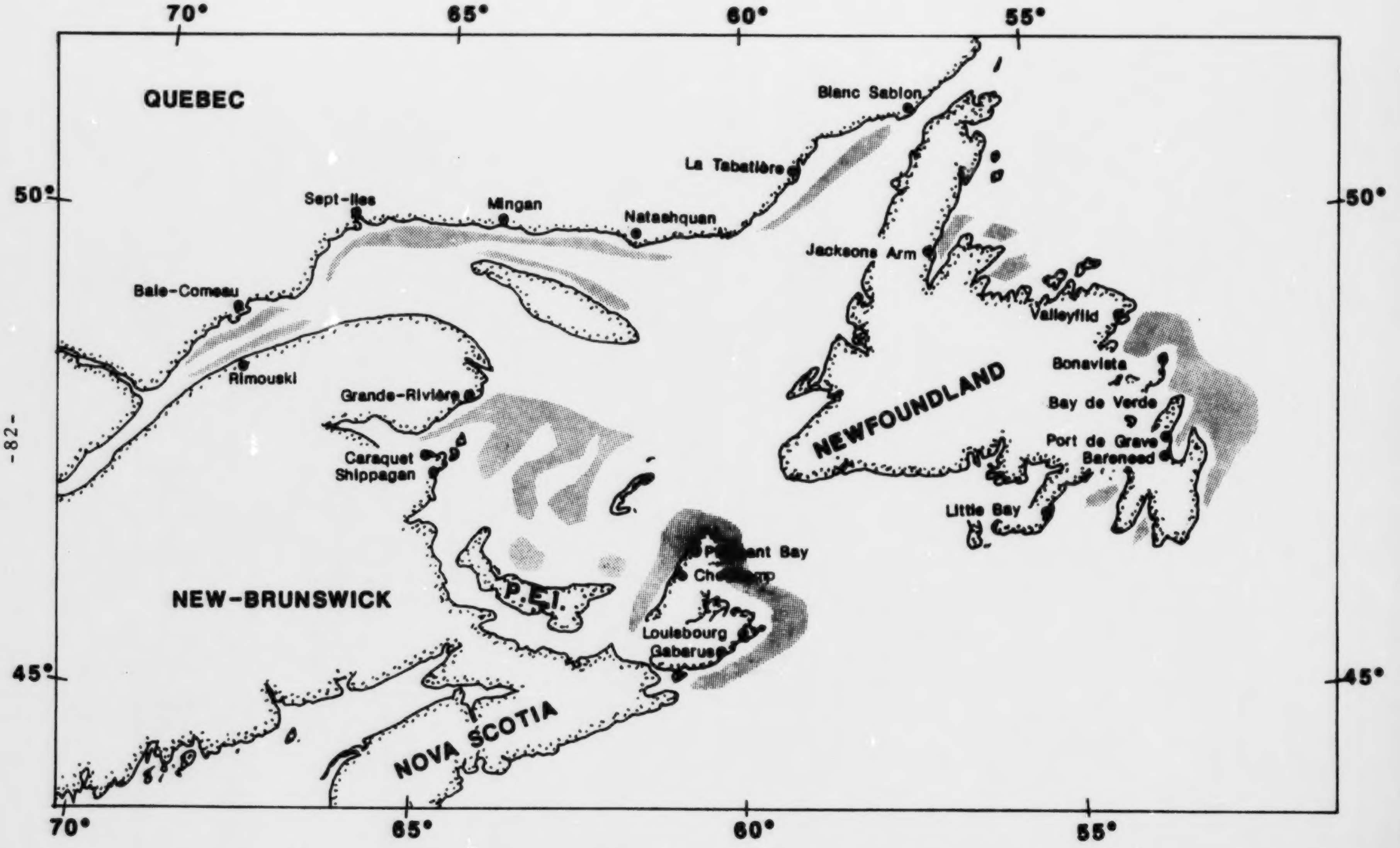

Fig. 1. Distribution of snow crab stocks (hatched zones) exploited in eastern Canada.

E. An Overview of Natural Mortality and Factors Affecting *Chionoecetes bairdi* and *C. opilio*

by D. Robichaud

INTRODUCTION

In recent years, *Chionoecetes bairdi* and *C. opilio* have been highly exploited. In some locations, these crab stocks have experienced dramatic declines (Otto et al. 1983, 1984), mainly attributed to intense fishing (Davidson and Comeau 1987; Mallet et al. 1988). However, natural mortality has not been ruled out as a significant contributor to observed declines, and our understanding of natural mechanisms that controls recruitment cycles and stock abundance remains poor. The following review documents various factors affecting natural mortality and the impact these could have on the abundance of crab stocks.

LOSS OF FERTILIZED EGGS

Recruitment trends for any crab stocks are ultimately linked to female reproductive potential. However, there is no complete understanding of the relationship between egg production and subsequent recruitment into the fishery for any crustacean species.

On the east coast of Canada and off the coast of Alaska, female *C. bairdi* and *C. opilio* are protected from the fishery (Colgate 1982; Elner and Robichaud 1983; Otto et al. 1983, 1984). The reproductive potential of the resource has been hypothesized to be unaffected by the commercial harvesting of males only (Watson 1970; Paul 1982; Elner and Gass 1984). However, there is an increasing concern about the instability of male-only crab fisheries (*Cancer magister*: Botsford et al. 1983; *Chionoecetes* sp.: Otto et al. 1983, 1984; Conan and Comeau 1986; *Paralithodes camtschatica*: Otto 1986).

Detailed sequence of events in mating behaviour has been described for *C. bairdi* (Adams 1982) and *C. opilio* (Watson 1970, 1972; Adams 1982; Hooper 1986). Females of both species reach a terminal size with the moult to maturity. Primiparous female crabs of both species mate immediately after the moult to maturity and extrude fertile eggs (Watson 1972; Paul 1982). Multiparous female *C. bairdi* and *C. opilio* can copulate in hard shell condition to obtain fresh sperm or can utilize sperm stored from previous matings to fertilize their eggs (Watson 1972; Paul 1982; Elner and Gass 1984; Paul and Adams 1984; Taylor et al. 1985; Hooper 1986). Recently mated, multiparous female *C. bairdi* and multiparous females that produce eggs fertilized with 1+ yr old sperm extrude egg clutches of similar sizes (Paul 1982). Adams and Paul (1983) have shown that mature males of all sizes are capable of producing an excess of sperm at mating and that 93% of mated females, following egg extrusion, had stored sperm.

Somerton (1982a) observed that while mature male C. bairdi of all sizes can mate, primiparous females have a tendency to mate with recently matured males and multiparous females tend to mate with larger males. Somerton and Meyers (1983) observed that in the eastern Bering Sea, primiparous female C. bairdi were approximately 70% as fecund as equal size multiparous females. Adams (1982) observed that multiparous female C. bairdi resisted mating attempts by small males, and that in competitions for females, larger males always won. Taylor et al. (1985) suggested that before fishing of larger males was established, this behaviour probably eliminated small males from much mating activity. According to Hooper (1986), male C. opilio may assist females in moulting and subsequently provide protection from predation, food, and assist in larval release. With such behaviour, significant removal of males could impact on recruitment.

The relationship between fecundity and female size varies between locations (Fig. 1) (Kon 1974; Haynes et al. 1976; Thompson 1979; Jewett 1981; Somerton 1981; Adams and Paul 1983; Davidson 1983; Elner and Gass 1984; Davidson et al. 1985). Differences can be attributed to season, egg stage, location, and whether females are primiparous or multiparous. Female C. opilio can lose up to 50% of deposited eggs during the course of embryonic development (Kon 1974; Elner and Gass 1984). A progressive decrease through the embryonic period in both intercept and slope of size versus fecundity suggests that egg loss may be proportionately greater for larger females (Kon 1974; Elner and Gass 1984). Egg loss has been attributed to both environmental factors, parasites, and diseases.

High population fecundity and egg production do not necessarily translate into high recruitment (Elner and Gass 1984). However, because of heavy exploitation of males, a close monitoring of population fecundity is justified.

LARVAL MORTALITY

Most benthic decapods have pelagic larvae which feed on plankton (Thorson 1964). Associated larval dispersal favours settlement in new, favourable habitats (Lanteigne 1985) but because it is unpredictable, planktonic larvae may have a high natural mortality (Thorson 1950). Consequently, larval abundance at settlement may be highly correlated to adult crab abundance (Lough 1976; Anger 1983).

Little is known about the magnitude of larval natural mortality for C. bairdi or C. opilio. Laboratory observations have provided detailed morphological descriptions of their four developmental stages (prezoea, zoea I, zoea II, and megalops), growth rate, feeding behaviour, and mortality in captivity (Kon 1979; Motoh 1973; Haynes 1973, 1981; Johnston 1976; Jewett and

Haight 1977; Paul et al. 1979b; Motoh 1982; Wencker et al. 1982; Incze et al. 1982; Davidson 1983; Incze and Paul 1983; Davidson et al. 1985). Some studies have investigated larval dispersion at sea and depth distribution in the water column according to crab larval stage and season (Ito and Ikehara 1971; Kon 1982; Roff et al. 1984; Lanteigne 1985; Roff et al. 1986; Incze et al. 1987). More recent studies on C. bairdi and C. opilio larval growth rate and relative abundance in the southwestern Bering Sea have shown a correlation between larval abundance and adult female abundance (Incze et al. 1984, 1987). However, data remains sparse on the impact of the environment on larvae (Kon 1973, 1982; Somerton 1982b; Lanteigne 1985), larval natural mortality (Smith et al. 1978; Jewett 1982), diel depth distribution, larval dispersal, larval growth, larval settlement patterns, and variability in larval abundance (Incze et al. 1987).

PREDATION

Off the west coast of Alaska, Chionoecetes bairdi and C. opilio have been shown to be the prey of 14 and 18 species of predators, respectively (Mito 1974; Jewett 1978; Smith et al. 1978; Feder and Paul 1980; Jewett 1982; Jewett and Feder 1982; Smith and Walters 1982). Some major predators are listed in Table 1.

On the east coast of Canada, only two major predators of C. opilio have been identified; the Atlantic cod, Gadus morhua, and the thorny skate, Raja radiata (Waiwood et al. 1980; Templeman 1982; Waiwood and Elner 1982; Lilly and Rice 1983; Lilly 1984; Lilly and Botta 1984; Waiwood and Majkowski 1984; Robichaud 1985; Robichaud et al. 1986).

In C. opilio, cannibalism has been observed by Powles (1968) on the east coast of Canada, and by Paul et al. (1979a) and Jewett and Feder (1982) in the Sea of Japan. However, cannibalism does not seem to be an important mortality component (Yasuda 1967; Brethes et al. 1984).

Little is known about the actual quantities of crab consumed by any predator. For example, Jewett's (1978) estimate off Kodiak Island of the number of C. bairdi consumed by Pacific cod, Gadus macrocephalus, was 326-times the estimated crab population. In the Gulf of St. Lawrence, Waiwood and Majkowski (1984) estimated that the biomass of C. opilio consumed by Atlantic cod approached that taken by the fishery itself. Waiwood and Elner (1982) and Waiwood and Majkowski (1984) hypothesize that higher predation has recently occurred in the Gulf of St. Lawrence because of increased crab recruitment caused by removal of older crabs by the fishery, and that Atlantic cod were simply reacting to the relative high availability of crabs in comparison to their other prey species. In contrast, Bailey (1982) suggested that Atlantic cod are an important cause of mortality and could be a major factor controlling the recruitment of C. opilio each year.

Ecological factors are also important. For example, Robichaud et al. (1986) have shown that the season during which the stomach samples are taken can influence results (Fig. 2). Atlantic cod captured during the spring had consumed a large quantity (40-66% by weight of total stomach contents) of large (75-110 mm carapace width [CW]), soft-shell male crabs, whereas cod captured in summer had consumed relatively less crab (2 to 14% by weight) but more smaller (5-46 mm CW) individuals. If weight is considered as a measure of predation, snow crab appear most vulnerable to cod during the crab moulting season. However, if the number of crabs consumed is considered most important, snow crabs were more vulnerable to cod predation during summer.

Currently, the actual impact that predation can have on crab stocks remains uncertain. However, it is known that predators of *C. bairdi* and *C. opilio* are many, and consequently, could have a significant impact on the magnitude of crab recruitment.

DISEASES AND PARASITES

Chionoecetes bairdi and *C. opilio* have both symbionts and parasites. Sparks and Hibbits (1979) and Hibbits et al. (1981) have identified the fungus *Trichomaris invadens* on the exoskeleton of *C. bairdi*. Surface encrustations, commonly called black mat syndrome (BMS), are unsightly and crabs with this condition are only reluctantly accepted by processors. Van Hyning and Scarborough (1973) initially named this fungus *Phoma fimeti*, and despite its appearance, concluded that it had no deleterious effect on *C. bairdi*. However, later studies have determined that BMS can cause massive destruction of the subepidermal tissue layers and possibly prevent moulting (Mix and Sparks 1980; Porter 1982; Sparks 1982). From a pot survey in the Gulf of Alaska in 1980-81, Hicks (1982) observed that 5% of males, 50% of females, and 90% of barren female *C. bairdi* had BMS. According to Hicks (1982), BMS can reduce clutch size and can prevent females from moulting and subsequently reaching maturity. Sparks (1982) concluded, based on the high incidence of infection and the hypothesized lethality of *Trichomaris invadens*, that BMS could be a significant cause of *C. bairdi* mortality, and that this fungus disease might be a significant factor in recent declines in *C. bairdi* abundance.

Two pathogenic bacteria (*Moraxella* and *Pseudomonas* spp.) have also been found in *C. bairdi* (Grischkowsky and Follett 1982). These bacteria can cause death under lab conditions, but the implications of these findings to wild populations has not been established.

There are no recent references on diseases or parasites of *C. opilio* from the west coast of Alaska. However, symbiotic species have been identified for *C. opilio* from the east coast of Canada. Hooper (1986) noted that *C. opilio* from Newfoundland had a diverse array of epizoic invertebrates living on their shells. The most common species were the bryozoan

(*Alcyonidium gelatinosum* (L.)), an unidentified athecate hydroid (possibly *Perigonimus* spp.), the hydroid *Hydractinia* sp., an unidentified amphipod, a tube dwelling polychaete, and leeches. Kahn (1982) identified four ecto-commensal organisms associated with *C. opilio* from Newfoundland: the leech *Johanssonia arctica*, a turbellarian platyhelminthes, an unidentified barnacle, and a bioluminescent polychaete. Steele et al. (1986) identified two commensal amphipods living on *C. opilio*, *Ischyrocerus commensalis* and *Gammaropsis inaequistylis*. Off the coast of Cape Breton, Brattey et al. (1985) found three symbiotic species living on *C. opilio*: leeches (*Johanssonia arctica*), polychaetes (*Eteonopsis geryonicola*), and turbellarians (*Ectocotyla* spp.). Ectocolylid turbellarians were previously observed on *C. opilio* in Chaleur Bay and Newfoundland by Flemming and Burt (1978).

INDIRECT FISHING MORTALITY

Off Newfoundland, a yearly loss of up to 876 t of *C. opilio* may result from the groundfish gillnet fishery (Miller and Hoyles 1973; Miller 1975). In addition, Miller (1975) estimated 15 t of crabs to be lost to trap ghost fishing and 264 t to handling of sublegal size crabs by crab fishermen. Loss due to handling is probably underestimated because this latter study was not conducted during the period of warmest temperatures or during the moulting period.

No other studies on crab loss due to indirect fishing mortality are known. However, some female and male snow crabs are captured yearly by Danish seiners and other groundfish trawl fisheries in the Gulf of St. Lawrence (unpubl. data). In recent years, indirect mortality caused by ghost fishing and rough handling of small crabs by fishermen has probably increased because of the increase in fishing pressure.

CONCLUSION

Overall, *Chionoecetes* natural mortality has been poorly studied. Particular life history stages or events (i.e. moulting) seem to be mostly associated with high mortality levels. Although intense fishing is probably a major cause of prerecruit crab mortality, natural mortality is still likely the major factor controlling crab recruitment, but the relative impact of the commercial crab fishery in relation to natural mortality is uncertain.

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Table 1. Major predators of *Chionoecetes bairdi* and *C. opilio* identified off the western coast of Canada and Alaska [modified table from Jewett (1982)].

Predator	Study area	Prey	Reference
Raja parmifera (Alaska skate)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Raja interrupta (Bering skate)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Microgadus proximus (Pacific tomcod)	Resurrection Bay, Gulf of Alaska	*C. bairdi* (megalopa)	A. J. Paul, pers. comm. 1982
Gadus macrocephalus (Pacific cod)	Kodiak Island shelf	*C. bairdi*	Feder and Jewett 1981 Jewett 1978
	Cook Inlet	*C. bairdi*	Feder et al. 1980
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Feder and Jewett 1980
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Myoxocephalus spp. (sculpins)	Kodiak Island shelf	*C. bairdi*	Jewett and Powell 1979
		C. bairdi	Feder and Jewett 1981
	Cook Inlet	*C. bairdi*	Feder et al. 1980
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Feder and Jewett 1980
		C. opilio and/or *C. bairdi*	Mito 1974
Malacocottus zonarus (sculpin)	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Hemilepidotus jordani (yellow Irish lord)	Kodiak Island shelf	*C. bairdi*	Jewett and Powell 1979
		C. bairdi	Feder and Jewett 1981
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974

Table 1. (cont'd)

Predator	Study area	Prey	Reference
Dasycottus setiger (spinyhead sculpin)	Northeast Gulf of Alaska	*C. bairdi*	Day (pers. comm.)
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Platichthys stellatus (starry flounder)	Cook Inlet	*C. bairdi*	Feder et al. 1980
	Northeast Bering Sea	*C. opilio* (megalopa)	Jewett and Feder 1980
Hippoglossoides elassodon (flathead sole)	Cook Inlet	*C. bairdi*	Feder et al. 1980
	Kodiak Island shelf	*C. bairdi*	Gray 1964
	Bering Sea	*C. opilio* and/or *C. bairdi*	Best 1981
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
	Far east seas	*Chionoecetes* spp.	Moiseev 1953
Lepidopsetta bilineata (rock sole)	Kodiak Island shelf	*C. bairdi*	Feder and Jewett 1981
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Glyptocephalus zachirus (rex sole)	Gulf of Alaska	*C. bairdi*	Smith et al. 1978
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi*	Mito 1974
Microstomus pacificus (Dover sole)	Gulf of Alaska	*C. bairdi*	Smith et al. 1978
Limanda aspera (yellowfin sole)	Kodiak Island shelf	*C. bairdi*	Feder and Jewett 1977
	Southeast Bering Sea	*C. opilio* and/or *C. bairdi* (megalopa)	K. Haflinger, pers. comm. 1982
Erignathus barbatus (bearded seal)	Southeast Bering Sea	*C. opilio*	Lowry et al. 1980

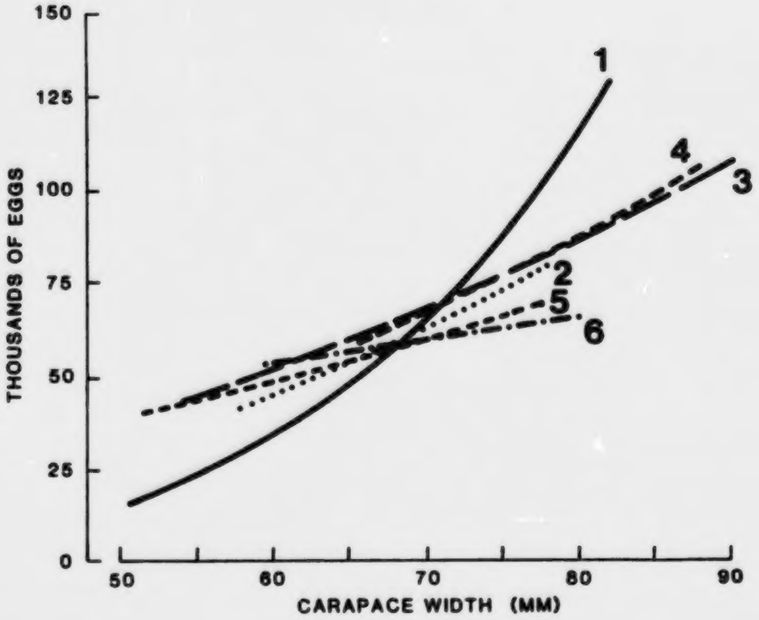

Fig. 1. Comparison between fecundity and female size for various locations on the east coast of Canada (after Elner and Gass 1984). 1, Gulf of St. Lawrence females (Haynes et al. 1976); 2, Newfoundland females; 3, northwestern Cape Breton Island females; 4, eastern Cape Breton Island females (Davidson 1983); 5, northwestern Cape Breton females without eyespot development; 6, northwestern Cape Breton females with eyespot development (Elner and Gass 1984).

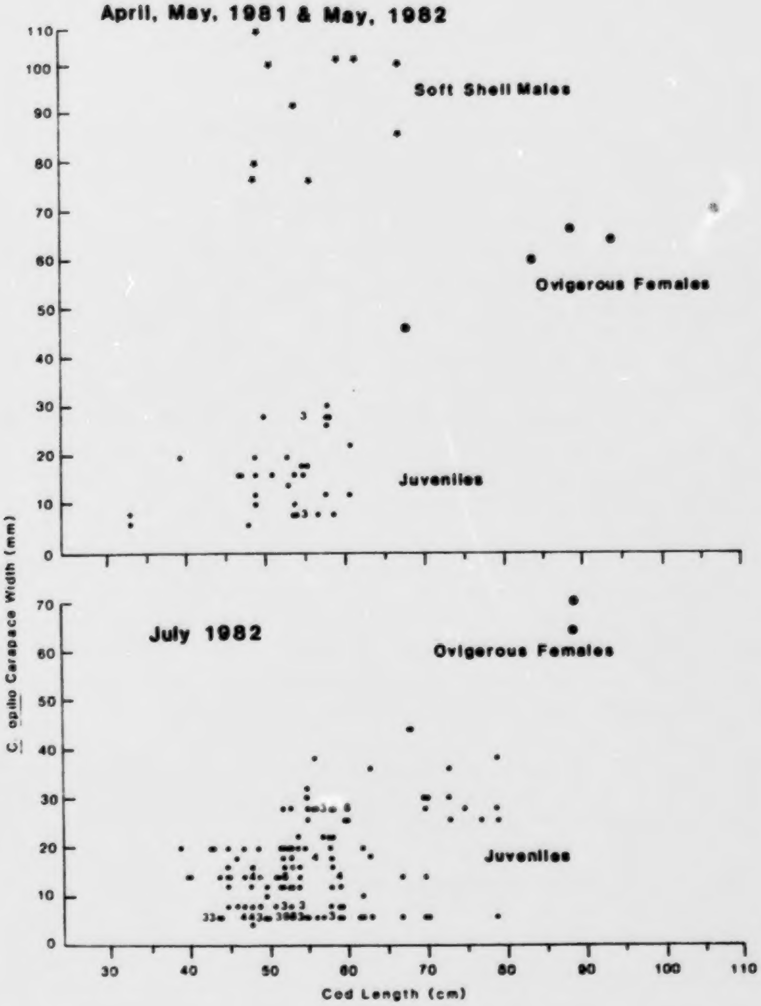

Fig. 2. Relationship between carapace width (mm) of C. opilio found in the stomach contents of cod, sampled during different seasons in 1981 and 1982, and the length (cm) of the cod (Robichaud et al. 1986).

III REVIEW OF LIFE HISTORY PATTERNS

A. Growth and Moulting Variables

Growth of Males after reaching Sexual Maturity in the genus *Chionoecetes*

by W.E. Donaldson

INTRODUCTION

Growth after sexual maturity has been an *a priori* assumption in the management of Alaska *Chionoecetes opilio* and *C. bairdi* fisheries, and conventional wisdom has probably played a role in maintaining this assumption. The Alaskan approach has been derived largely from the management of king (*Paralithodes* sp.) and Dungeness (*Cancer magister*) crab fisheries. Management philosophies to a large extent are derived from what we know about other species' life histories, and are easily transferred to a new commercial species where little life history information is initially available. As this "new" fishery develops, we hopefully test the transferred concepts and build a unique management approach for each new species of commercial interest.

Conan and Comeau (1986) have challenged the validity of the conventional dogma, which currently assumes male *Chionoecetes opilio* continue to moult after achieving sexual maturity. If their hypothesis of a terminal moult is correct, this would be a significant advance in the understanding of snow crab life history and, as discussed in their paper, may have significant impacts on present management strategies.

In this paper, I address whether male growth continues after sexual maturity. My intention here is to summarize the data that is in support of this hypothesis, which is based on three types of information: 1) the literature on *C. opilio*, 2) unpublished *C. opilio* data, and 3) the literature and unpublished data for congeneric species.

Published data on *C. opilio*

Adams (1979) states in a summary of the *C. opilio* literature that "several researchers" (Kon, Watson, Ito, and Sinoda - to name a few) have separately evaluated the duration of each stage of development and the longevity of *C. opilio*. Ito (1970) assigned a summed duration of one year to juvenile instar stages I, II, III and IV; 16 months to instar stage V; and approximately 12 months to each later stage. This recognizes a post puberty moulting schedule. For male crabs with carapace widths (CW) >100 mm (adult II stage and greater), Watson (1969) believed that a biennial moulting period is more likely. After mark-recapture studies of *C. opilio* in Wakasa, Niwa (1967) concluded that adult males require at least two years between each moult. Also, Kobayashi (1965) conducted mark-recapture studies which indicated that adult males moult once each year. These four researchers concluded, after independent studies, that the growth rate of C. opilio decreases during the last several moults before the moult to maturity. Female crabs undergo a terminal moult at morphometric maturity, while adult males grow at a decreased (but relatively uniform) rate and probably undergo at least two post-puberty moults.

Miller and Watson (1976), in a laboratory study of C. opilio from the Gulf of St. Lawrence, concluded that growth per moult for mature males averages 18.4%. However, he also noted that crabs with old, encrusted shells may have reached a terminal moult stage. Of his aquaria-held crabs >70 mm CW, no crabs with old shells moulted in the laboratory whereas those with new shells did. Miller noted, however, that crabs >90 mm CW were held in aquaria for more than a year before moulting. He concluded by stating that data on moulting frequency based on the artificiality of the lab environment are suspect due to the potential reluctance of large individuals to moult in confinement.

In summary, the literature supports a life history scenario of similar growth rates for juvenile male and female C. opilio, a terminal moult for females at maturity, and a post-puberty moulting schedule with protracted intermoult periods for males. Post-puberty moulting events may be described as episodic in nature.

Unpublished data on C. opilio

Observations on the shell age of male, Bering Sea C. opilio do not support the concept of a terminal moult at maturity. Figures 1 to 14 depict the shell age of male C. opilio crab captured during National Marine Fisheries Service (NMFS) research surveys (Robert Otto, Box 1638, Kodiak, Alaska 99615, unpubl. data). I initiate this data series with the 1974 survey year data because C. opilio was not then a targeted species, and therefore bias from fishing had not yet occurred. The size at which 50% of male C. opilio are mature is estimated to be 65 mm CW (Somerton 1981) (Fig. 15). If the moult to maturity is a terminal moult, and in the absence of heavy exploitation, we would expect to observe a large accumulation of oldshell males in the mature portion of the population in the early years of the fishery. Figures 1 to 14 show this was not the case. The majority of large crab are new shell animals, implying recent moulting activity. Similarly, ageing of crab caught in the commercial fishery, which targets on large males(≥100 mm CW), shows that the population is composed of a high percentage of newshell crab or post puberty moulting animals (Table 1).

In 1980 (Fig. 7) and 1986 (Fig. 13), there was an increase in skip-moulting with size, and presumably a buildup of terminally moulting crab. However, examination of data in the following year, 1981 (Fig. 8) and 1987 (Fig. 14), respectively, it appears as though an episodic moulting event occurred and the population was moving back to a post-puberty moulting state. We know from limited tag returns that large *C. opilio* in the Bering Sea do in fact moult (Fig. 15, Table 2).

DATA ON CONGENERIC SPECIES

In a study by Adams and Paul (1983), male *C. bairdi* that were 65-70 mm CW width mated. These mating male crabs were morphometrically immature, i.e. in a preterminal moult condition. Since this study A. J. Paul (Box 730, Seward, Alaska 99664) has documented moulting subsequent to mating in *C. bairdi* (pers. comm., 1987). According to Colgate and Hicks (1983), crabs of this size and one cohort group larger are almost always new-shell animals, suggesting that they are not anecdysic. Additional support for moulting after morphometric maturity is evident in a study involving the aging of barnacles found on *C. bairdi* (Paul and Paul 1986). Eighty-seven percent of terminal moult female crabs from Cook Inlet, Alaska, were carrying barnacles, and 42% of the female crab had barnacles that had survived three or four growing seasons. However, none of the 1,180 males examined carried barnacles three or more growing seasons old. The males ranged in size from 140-190 mm CW (morphometrically mature animals). If mature males terminally moult at the moult to maturity as do females, we would expect the age composition of settling barnacles to be similar between the sexes of *C. bairdi*. Also, Tester and Carey (1986), in a study of *C. tanneri*, stated, "observations on general carapace condition and abundance of epifauna indicate that adult male *C. tannerri* do moult frequently enough to maintain their carapaces relatively free of epifauna and lesions caused by bacterial infection".

Additionally, it has been demonstrated that morphometrically mature *C. bairdi* moult (Donaldson and Johnson 1987), using the statistical techniques described by Conan and Comeau (1986).

I have only presented data here that supports post-puberty moulting, since Conan (this volume) has presented data in support of a male terminal moult hypothesis. I am aware that there are strong arguments supporting the terminal moult concept; however, acceptance of a new convention requires truly compelling evidence. I feel that the supporting literature presents a strong case for post-puberty moulting, i.e. no terminal moult in males, in *C. opilio*. A number of researchers have reached this conclusion from completely independent studies and in addition, there is supporting data from closely related species, *C. bairdi* and *C. tanneri*, that supports this hypothesis. In summary, then, I believe the data available suggests that mature male *Chionoecetes* do not terminally moult at the moult to maturity.

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Table 1. Historic annual Bering Sea *C. opilio* catch statistics. NA = not available.

Year	No. Vessels	No. Landings	No. crab[1]	Landed weight (t)[1]	Weight deadloss (t)	Pots Lifted	Average CPUE (crab per pot)	% New Shell[2]	Avg. wt. (kg)	Avg.[2] Width (mm)
1977-78	15	38	1,267,546	778.4	-0-	13,247	96	NA	.63	NA
1978-79	102	490	21,567,656	14,255.6	300.0	190,746	113	83.0	.68	113.1
1979-80	134	596	24,286,779	17,950.0	103.6	255,022	95	90.0	.72	118.1
1981	153	867	34,415,322	23,937.3	1,029.7	435,742	79	79.2	.68	117.0
1982	122	803	24,084,984	13,313.74	470.8	469,091	51	78.0	.54	109.4
1983	109	462	23,838,149	11,851.8	600.8	287,127	83	NA	.50	NA
1984[3]	52	367	24,009,935	12,162.3	362.3	173,591	138	78.0	.50	105.4
1985[4]	75	718	52,903,246	29,936.9	482.7	372,045	120	80.0	.59	108.0
1986[5]	88	992	76,499,123	44,445.5	631.8	543,744	141	73.7	.59	109.5
1987	103	1,038	81,307,659	46,223.1	443.8	616,113	132	83.0	.59	108.7

[1] Deadloss included.

[2] Southeast and Pribilof Districts only.

[3] North of 58°N reopened until 12/31.

[4] West of 164°W opened through 12/31.

[5] Open only west of 164°W.

Table 2. Growth data from 1978-1982 _C_. _opilio_ tag recoveries, Bering Sea.

Release Date	Recovery Date	Initial CW (mm)	Final CW (mm)	Growth (mm)	% Increase	Time at large (days)
5/31/80	6/15/80	108	123	15	13.9	15
5/28/80	5/04/81	110	117	7	6.4	341
5/28/80	4/13/81	112	129	17	15.2	320
5/22/80	5/08/81	114	137	23	20.2	351
5/31/80	3/14/81	115	125	10	8.6	287
5/28/80	4/20/81	124	140	16	12.9	327
5/20/80	5/09/82	97	107	10	10.3	719

National Marine Fisheries Service Data

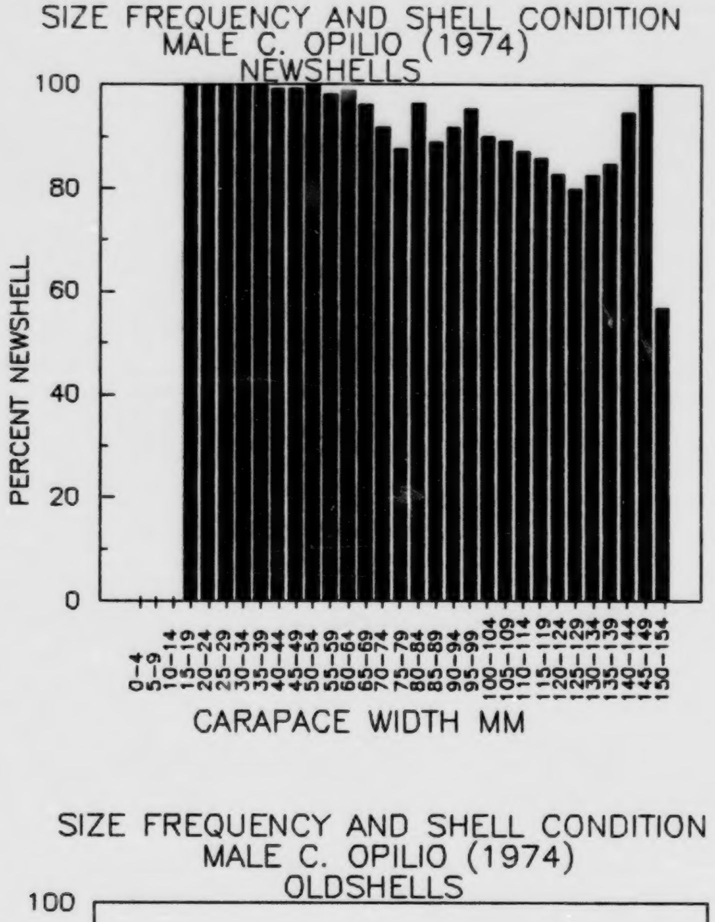


Fig. 1. NMFS Bering Sea _C_. _opilio_ survey data.

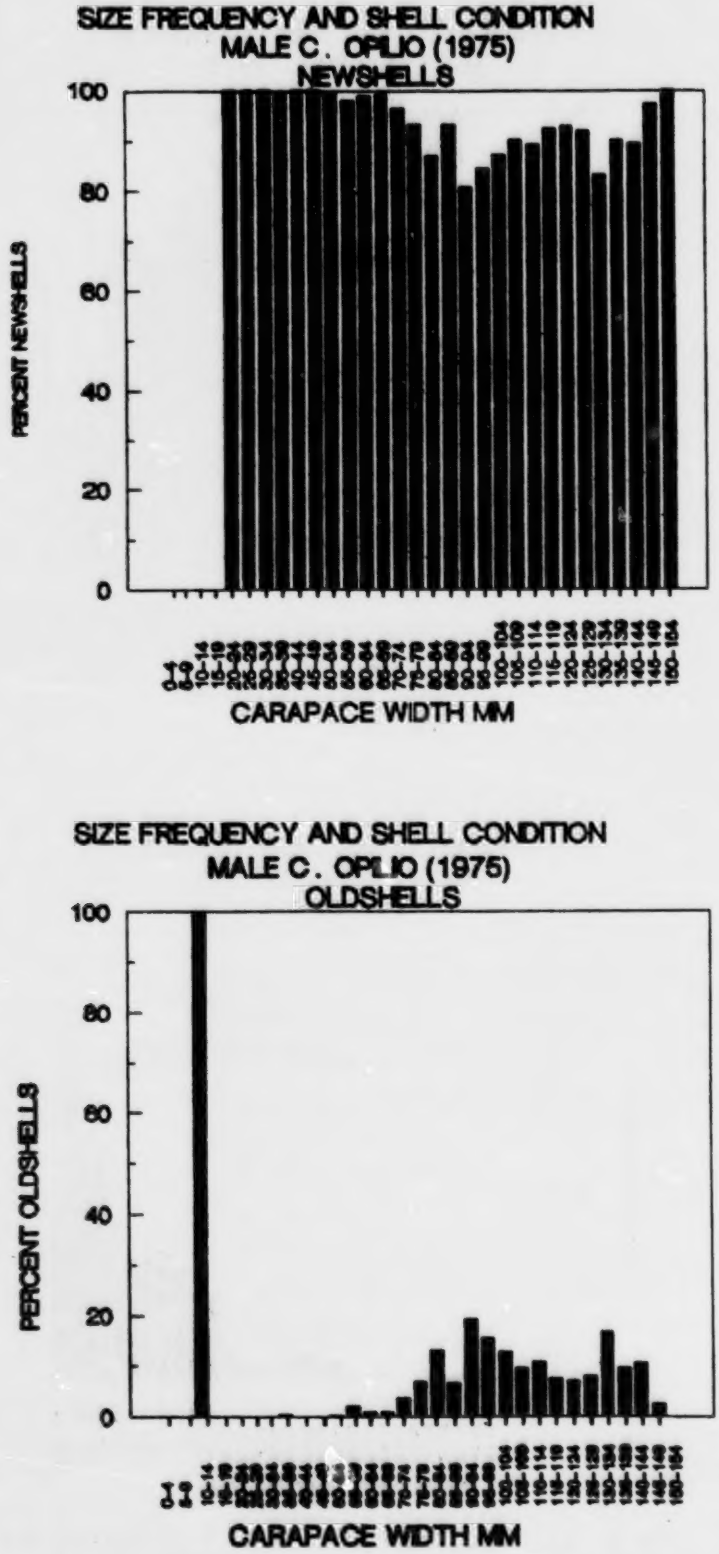
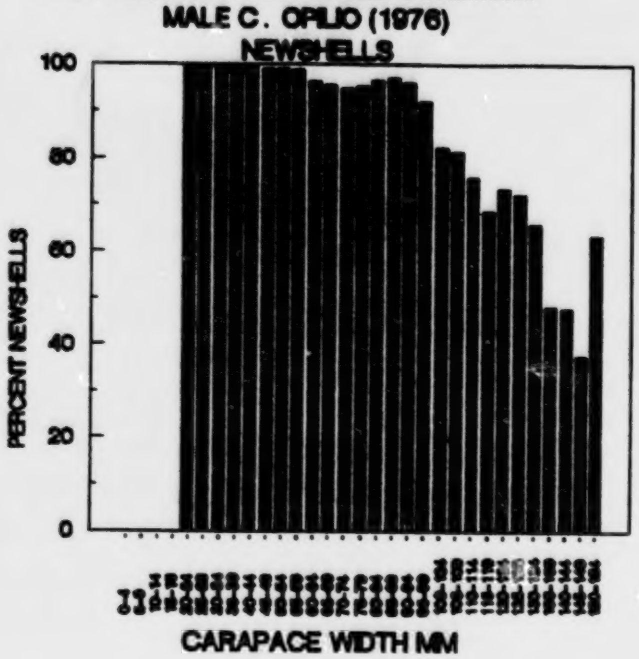


Fig. 2. NMFS Bering Sea _C_. _opilio_ survey data.



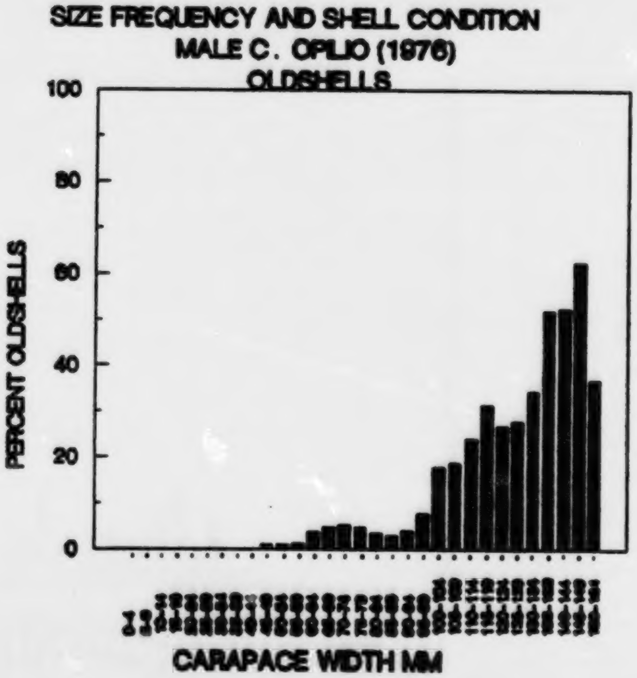


Fig. 3. NMFS Bering Sea *C. opilio* survey data.

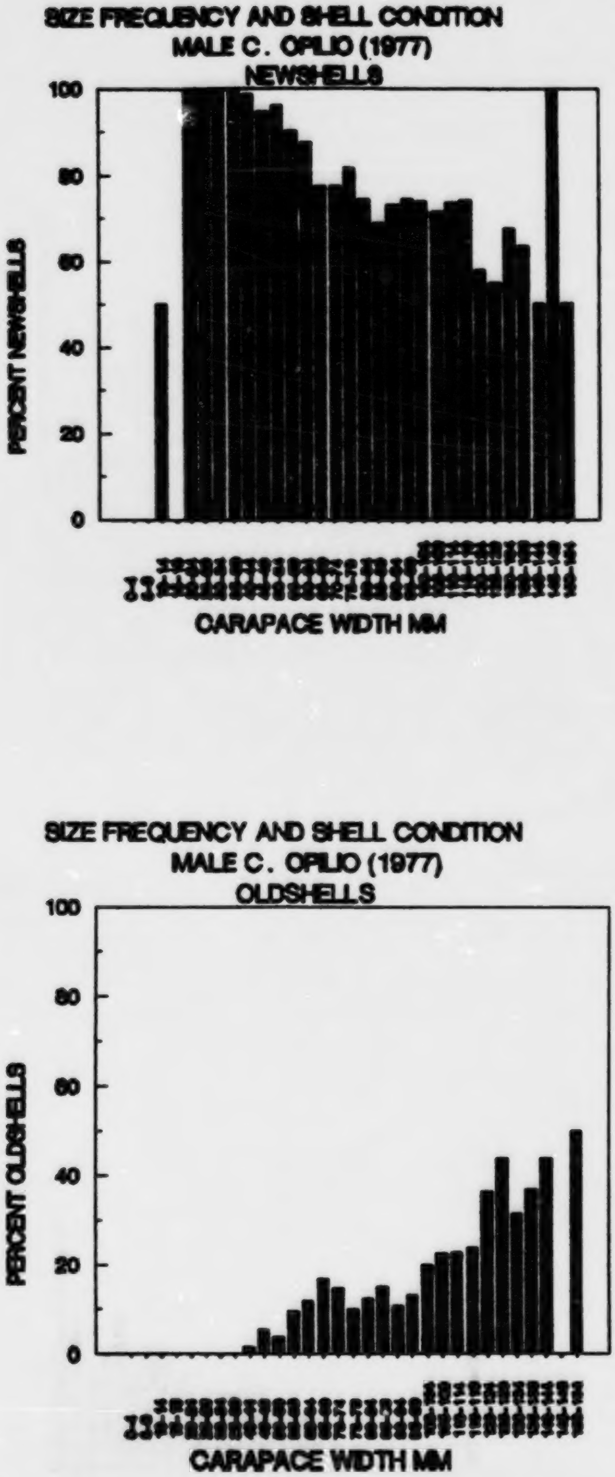
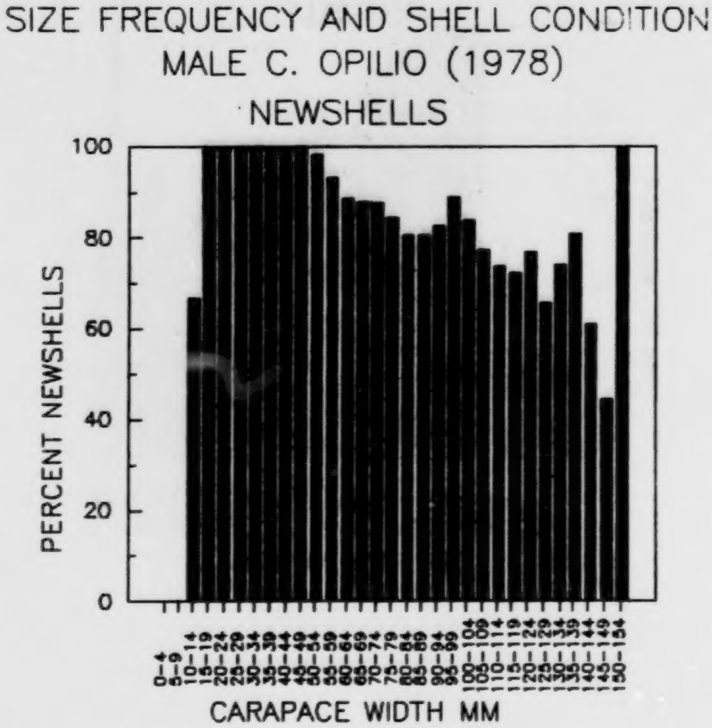


Fig. 4. NMFS Bering Sea _C_. _opilio_ survey data.



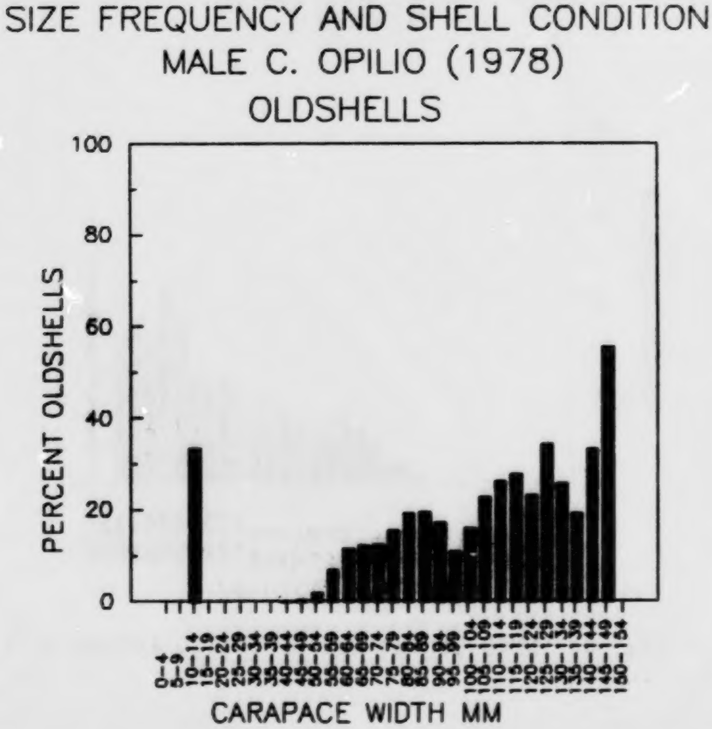


Fig. 5. NMFS Bering Sea C. opilio survey data.

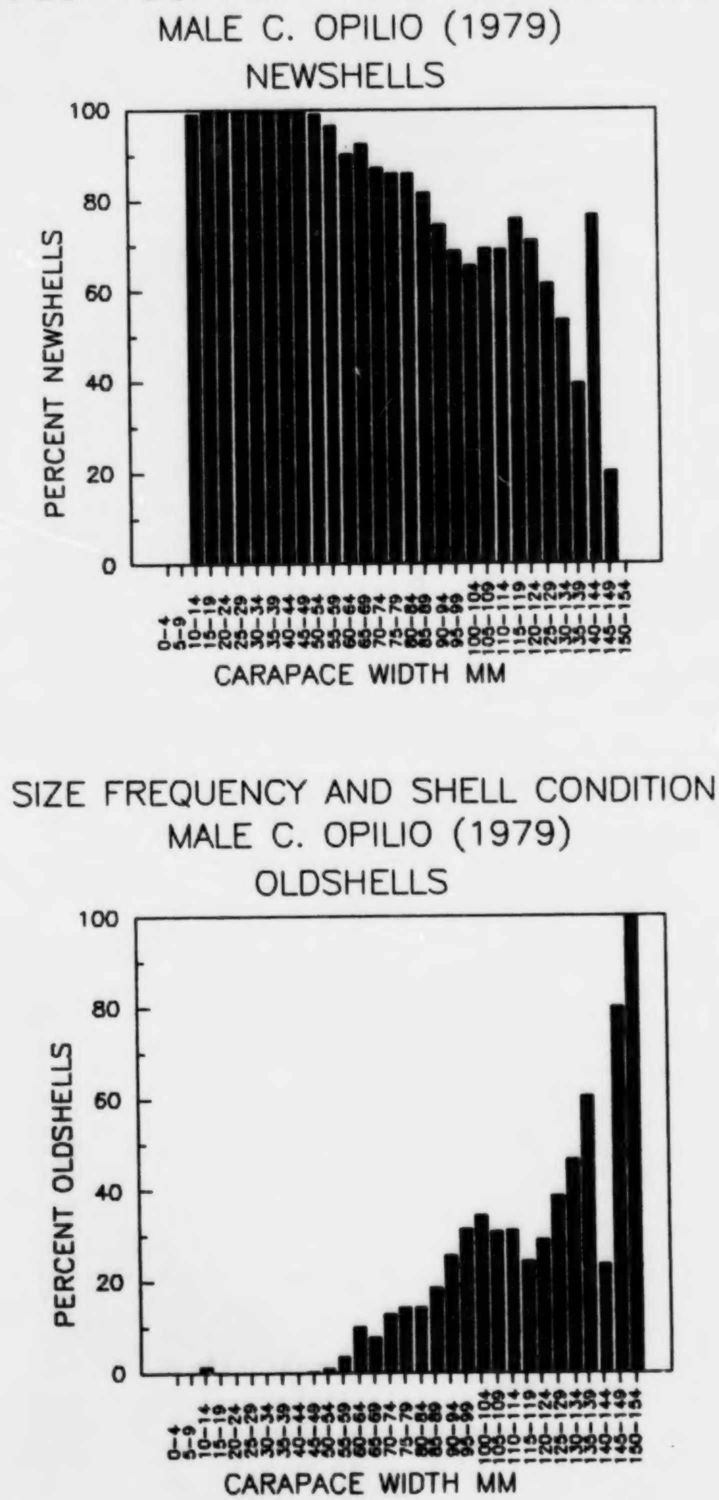
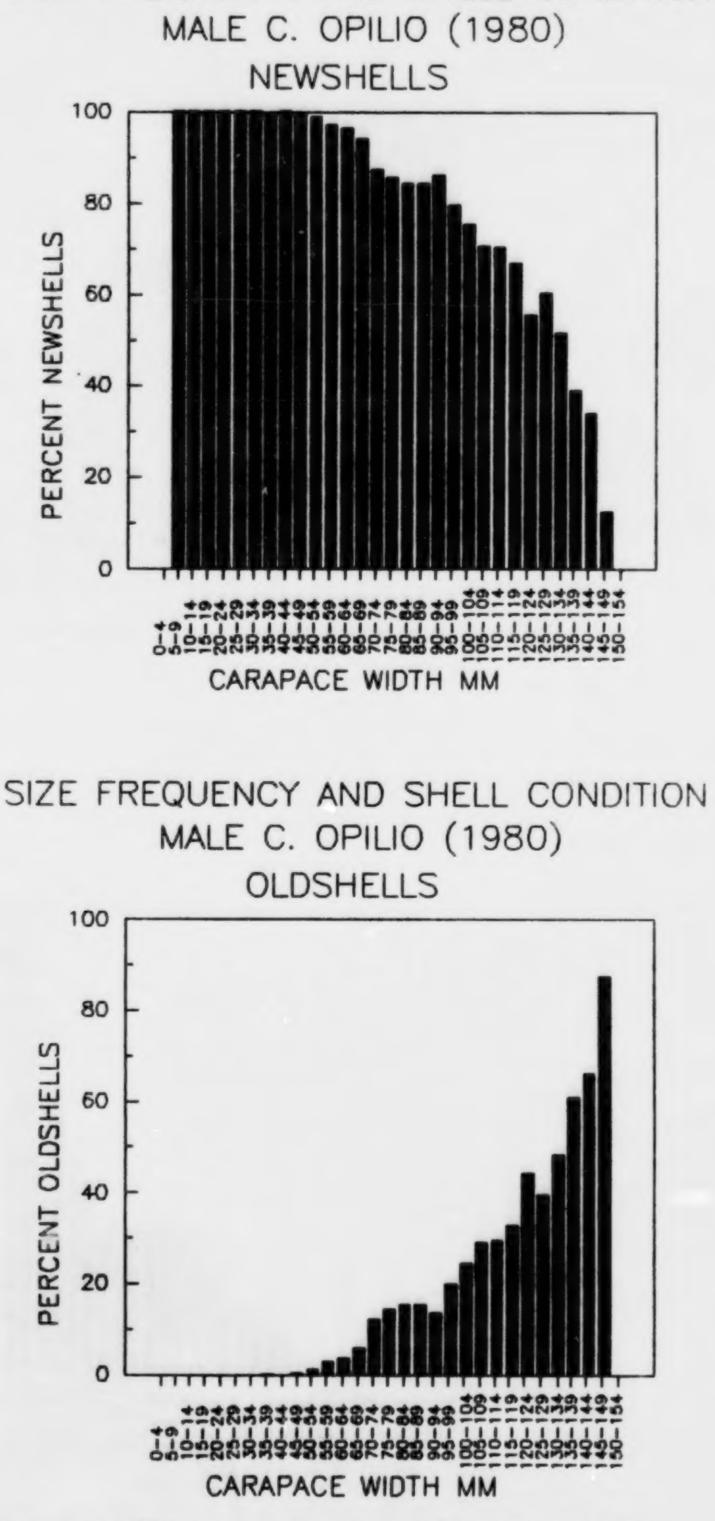


Fig. 6. NMFS Bering Sea *C. opilio* survey data.



SIZE FREQUENCY AND SHELL CONDITION
MALE C. OPILIO (1980)
NEWSHELLS

SIZE FREQUENCY AND SHELL CONDITION
MALE C. OPILIO (1980)
OLDSHELLS

Fig. 7. NMFS Bering Sea _C_. _opilio_ survey data.

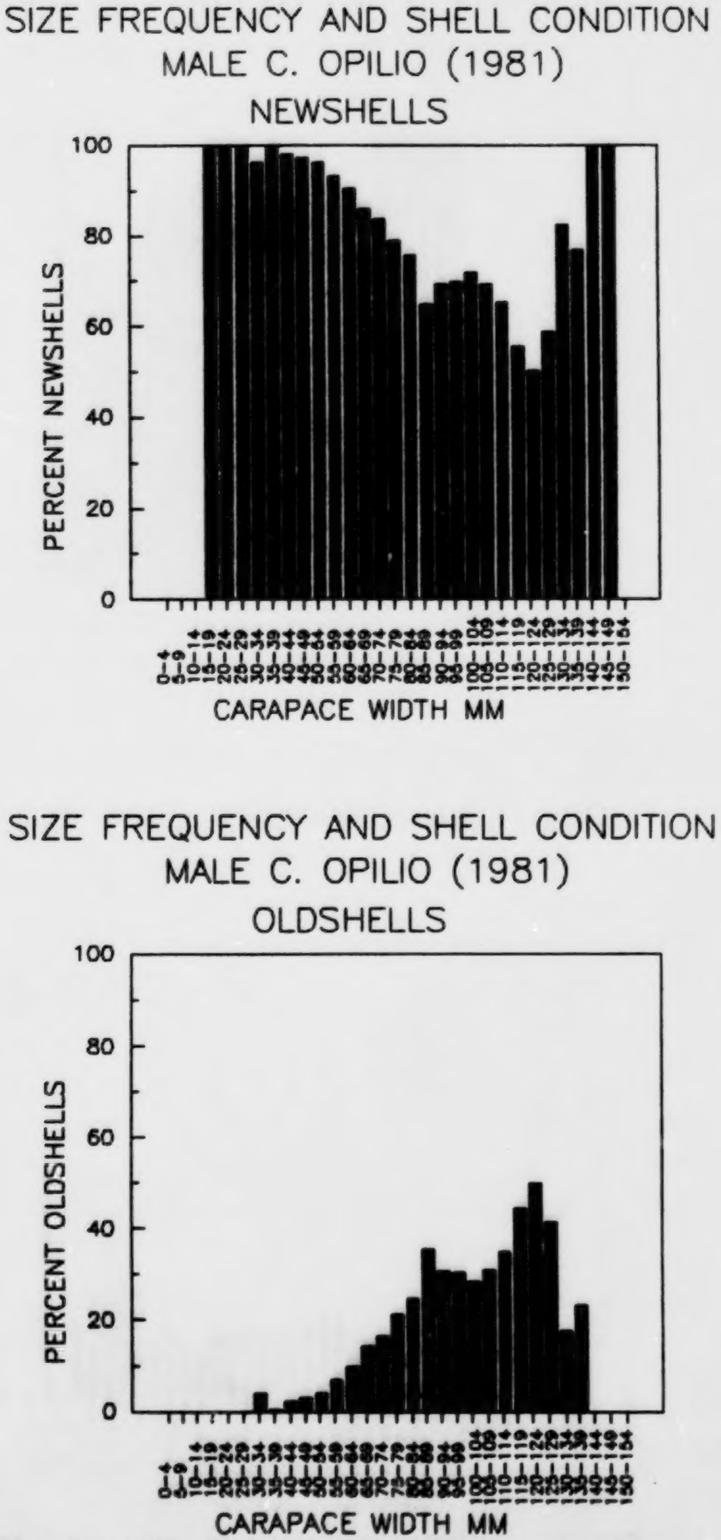
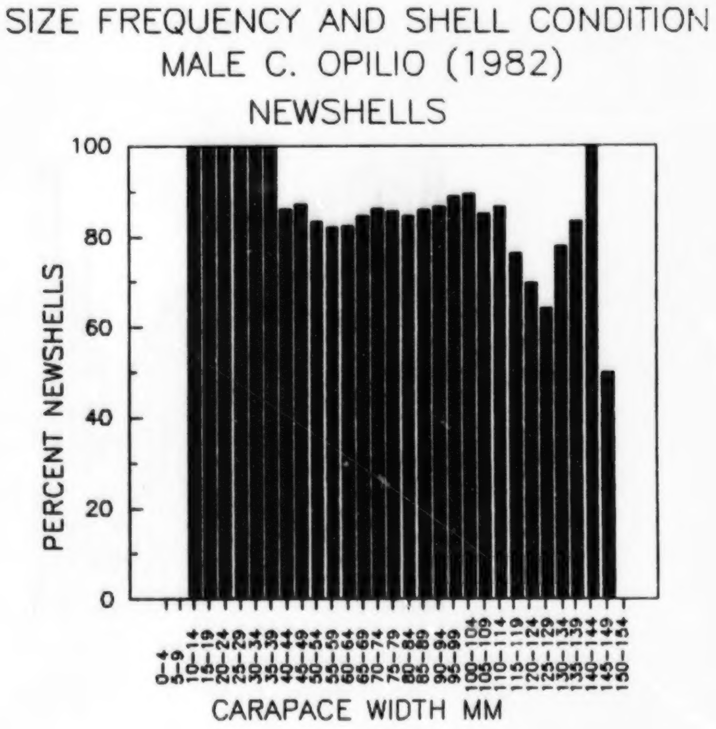


Fig. 8. NMFS Bering Sea C. opilio survey data.



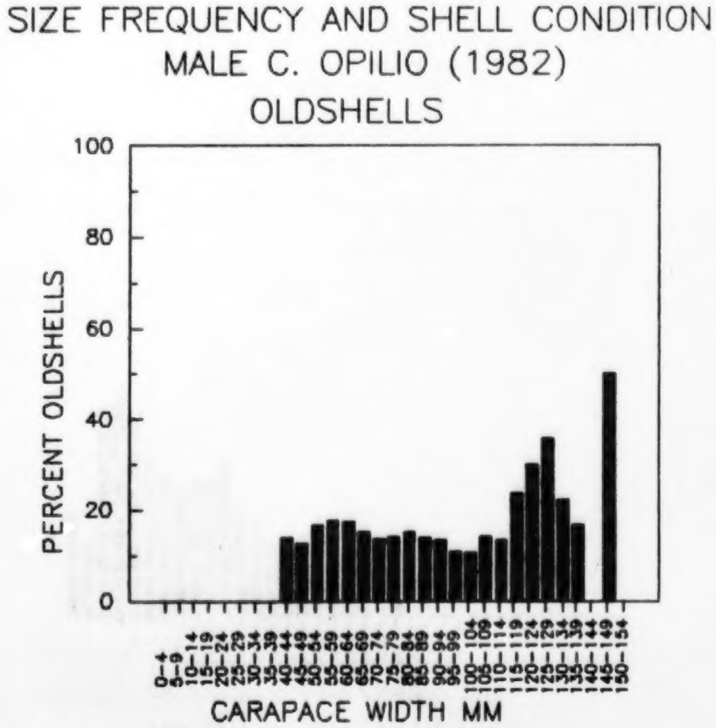


Fig. 9. NMFS Bering Sea _C_. _opilio_ survey data.

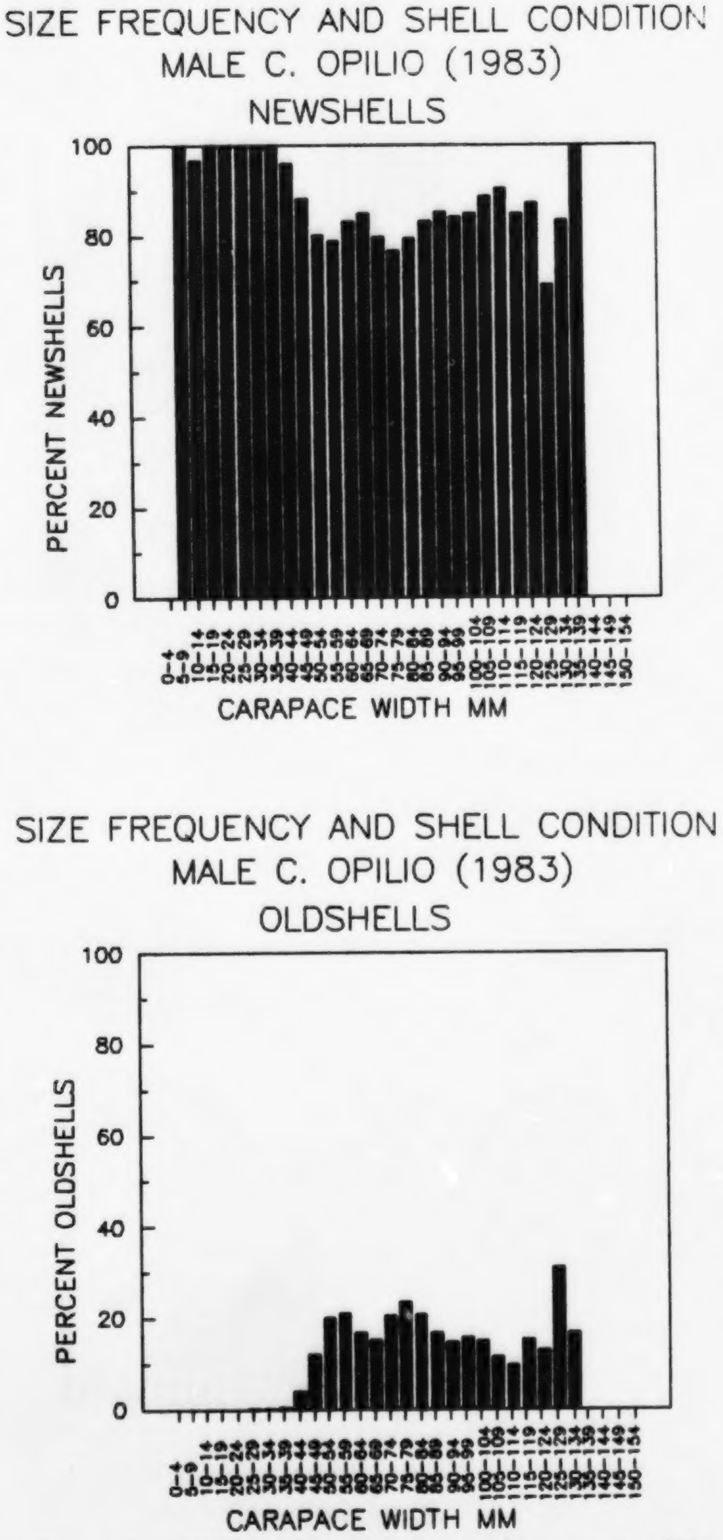


Fig. 10. NMFS Bering Sea C. opilio survey data.

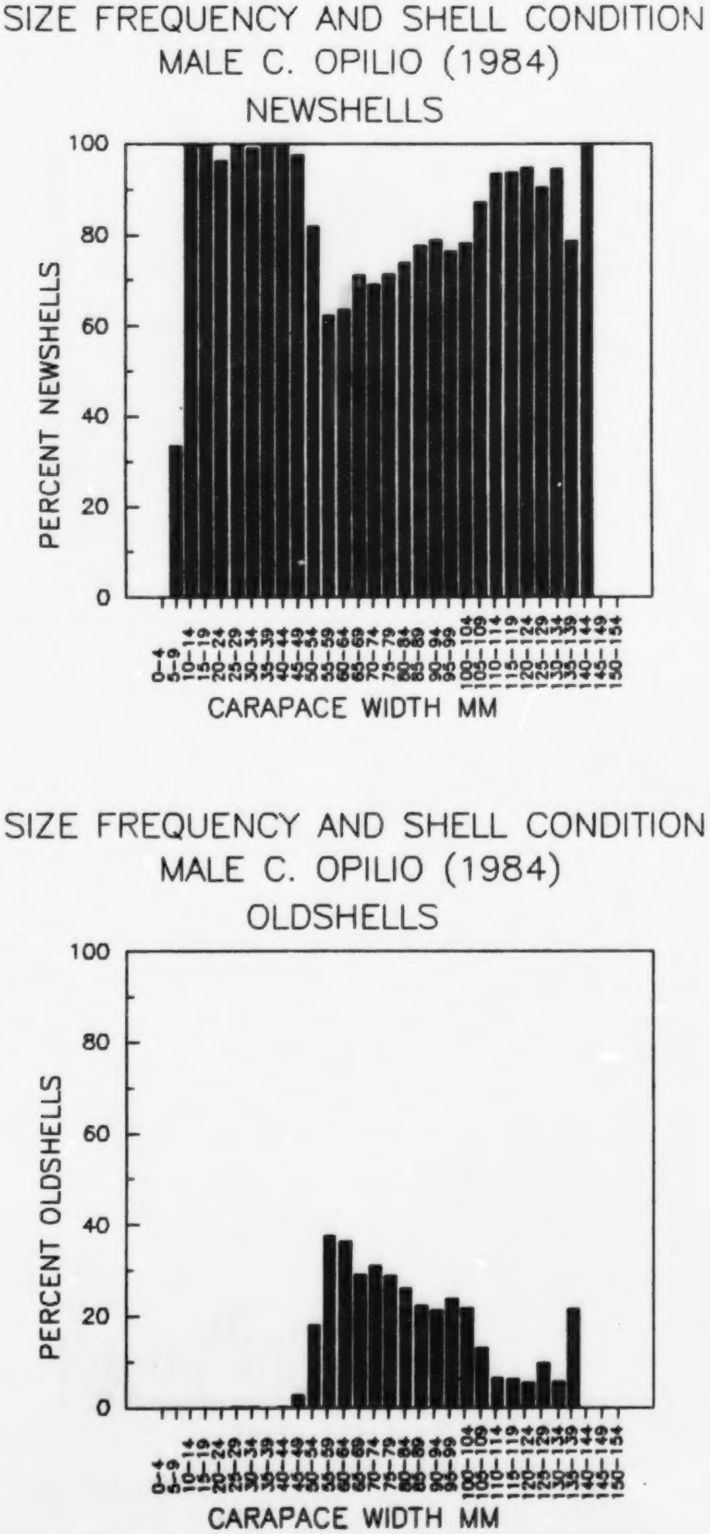


Fig. 11. NMFS Bering Sea *C. opilio* survey data.

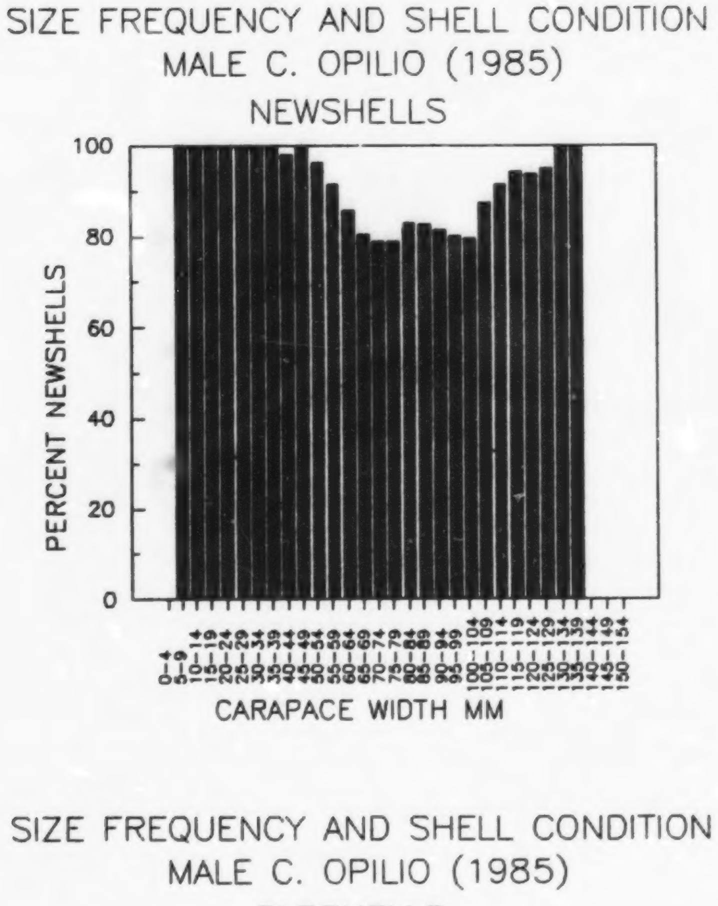
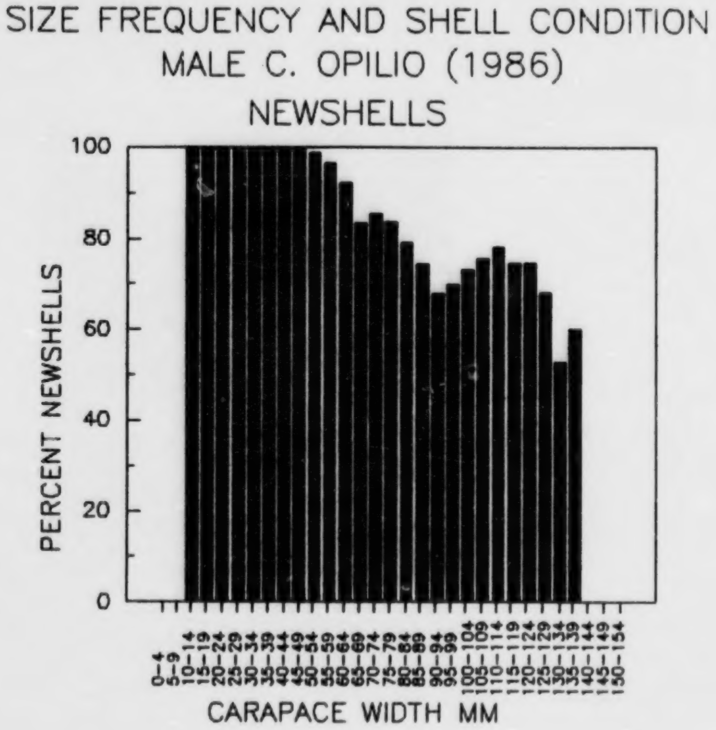


Fig. 12. NMFS Bering Sea *C. opilio* survey data.


SIZE FREQUENCY AND SHELL CONDITION
MALE C. OPILIO (1986)
NEWSHELLS

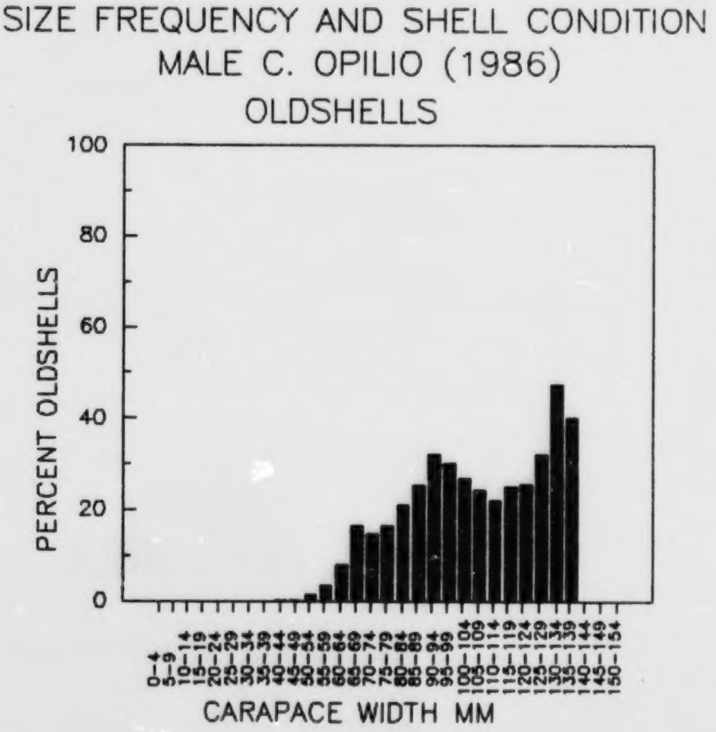
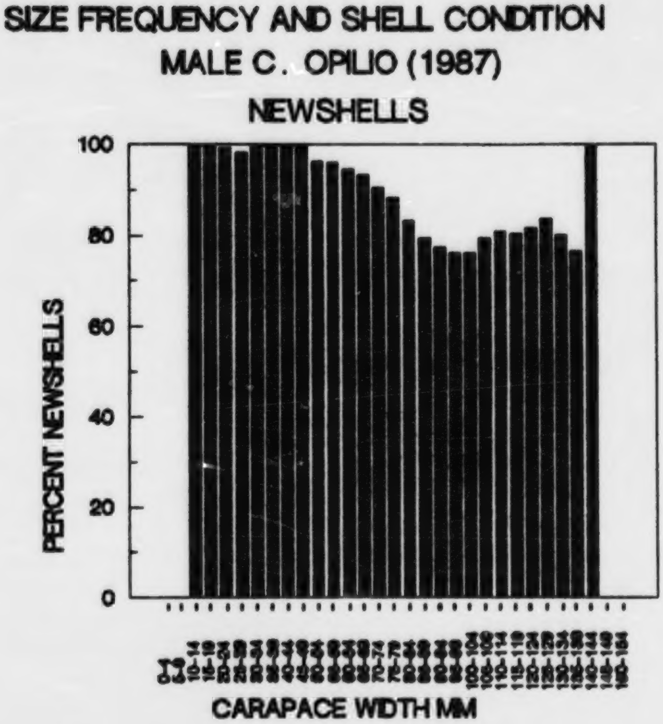

SIZE FREQUENCY AND SHELL CONDITION
MALE C. OPILIO (1986)
OLDSHELLS

Fig. 13. NMFS Bering Sea C. opilio survey data.



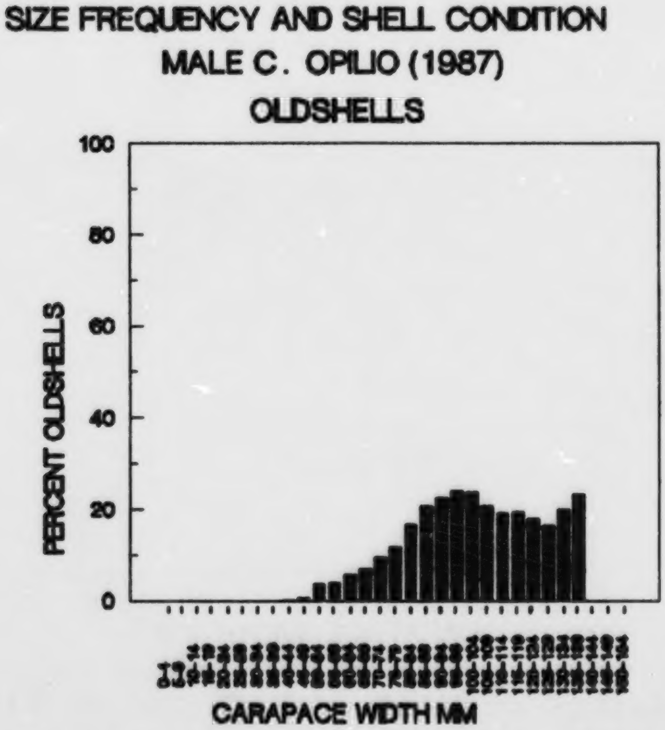


Fig. 14. NMFS Bering Sea _C_. _opilio_ survey data.

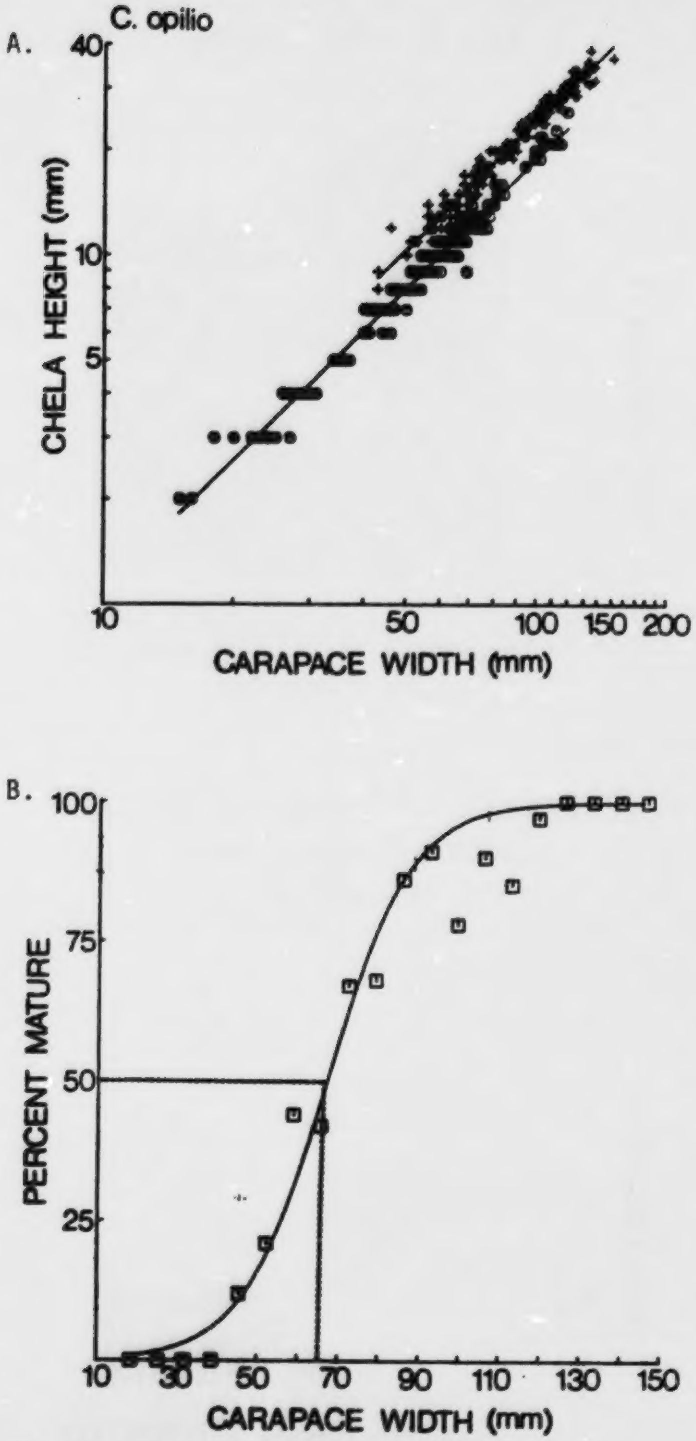


Fig. 15. A. Classification of chela height and carapace width measurements into adults (+) and juveniles (o). B. The fit of the logistic equation to the percent mature as a function of size for *C. opilio* (from Somerton 1981).

B. Variables Affecting Recruitment

H_0: Density-dependent Factors have No Impact on the Level of Annual Recruitment to the Commercial Fishery

by G.P. Ennis

INTRODUCTION

There have been few detailed studies dealing with stock-recruitment relationships in decapod crustacea and consequently, knowledge and understanding of recruitment dynamics is generally very limited. Both density-independent and density-dependent effects are evident in most cases where the relationship has been examined in a sufficiently detailed and comprehensive manner. In most cases there has been little resolution of the mechanisms involved in either process or how they operate at different life-history stages.

DISCUSSION

There is good evidence that recruitment of the blue crab, Callinectes sapidus, on the east coast of the United States is primarily determined by density-independent effects operating on larval stages (Johnson et al. 1984; Sulkin and Epifanio 1986). In shrimp as well, recruitment appears to be determined primarily by density-independent effects (Garcia 1983; Pauly 1982; Penn and Caputi 1986). In Dungeness crab, Cancer magister, populations on the northwest coast of the United States, both density-independent effects operating on larval stages and density-dependent effects operating on post-larval stages (i.e. between settlement and recruitment to the fishery) appear to contribute greatly to the recruitment variation (Botsford 1986 a,b). In the Western Australian rock lobster, Panulirus cygnus, density-independent effects and an apparently strong stock-dependent (a form of density-dependent) effect operate on larval stages; after settlement, density-dependent effects are primarily responsible for regulating recruitment to the fishery (Chittleborough 1979; Morgan et al. 1982). In the American lobster, Homarus americanus, it appears that density-independent effects operate on larval stages and, subsequent to settlement, density-dependent effects seem to be primarily responsible for recruitment regulation (Fogarty and Idoine 1986).

In few of the foregoing studies were the mechanisms involved in density-dependent regulation established. In addition to density-independant effects, stock-dependent mortality during the larval stages of the Western Australian rock lobster results in a much lower abundance of puerulus (settling stage) being produced when abundance of spawning females, and hence larval production, is high (Morgan et al. 1982). The underlying mechanisms are unknown but may be related to increased levels of predation or cannibalism at high levels of larval abundance. It has been demonstrated that among juvenile rock lobsters, which occupy shallow nursery reefs for 4 to 5 years before recruiting to the fishery, natural mortality is increased and growth rate is decreased at high densities, apparently due to limitations in availability of food and shelter (Chittleborough 1979). In the case of the American lobster, Fogarty and Idoine (1986) postulate that shelter is the key limiting resource involved in density-dependent regulation of recruitment subsequent to larval settlement.

There have been no detailed studies of stock-recruitment relationships for species of *Chionoecetes*. On the basis of the foregoing, it may be that stock-dependent mortality is important during the larval period, and that the abundance of settling stage larvae (megalopae) is generally low due to continuous high larval production because females are not commercially exploited. Density-dependent processes operating subsequent to larval settlement may also be involved in regulating recruitment.

This review of whether density-dependent factors have an impact on recruitment to the snow crab fishery focuses rather narrowly on subcommercial male crabs within one moult increment of the 95 mm minimum legal size, i.e. prerecruits. Growth and survival within the prerecruit portion of the population in a given year, as well as prerecruit abundance, will determine recruitment to the commercial fishery.

There is little information available in the literature for *Chionoecetes* which indicates whether there is a density-dependent effect on growth and survival among prerecruits. *Chionoecetes* are important prey for a variety of fish and they are also cannibalistic (Jewett and Feder 1982; Waiwood and Elner 1982). Whether density affects these interactions, and hence, growth and survival within the prerecruit portion of a snow crab population, is unknown. Both the Western Australian rock lobster and the American lobster are critically dependent on bottom types that provide suitable shelters. In these species, food and shelter appear to be limiting factors which have a density-dependent effect on growth and survival. In *C. opilio*, it has been suggested that settlement onto bottom composed of course sediment (pelitic gravel and muddy sand) would favor survival by providing better protection against predators and a better selection of food for small individuals (Desrosiers et al. 1982; Brêthes et al. 1982; Brêthes et al. 1984). Larger juveniles apparently move into deeper water onto bottom composed of finer sediment (Desrosiers et al. 1982; Coulombe et al. 1985; Bouchard et al. 1986). It seems unlikely that this kind of bottom is sufficiently limited in terms of suitable space to adversely effect growth and survival of prerecruits, although food supply could be a limiting factor.

In the absence of detailed studies of the stock-recruitment relationship or of aspects of the dynamics of recruitment in *Chionoecetes* spp., conclusions with respect to the hypothesis that density-dependent factors have no impact on the level of annual recruitment to the commercial fishery have to be based primarily on inferences from studies of other decapod crustaceans. It seems likely that density-dependent processes operating subsequent to larval settlement affect recruitment to the fishery. Recently settled and early juvenile stages are likely to be most involved, but there is presently no clear evidence of a density-dependent effect influencing the level of annual recruitment to the fishery.

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H_0: Density-dependent Factors have No Impact on the Level of Annual Recruitment to the Commercial Fishery

by E.G. Dawe

INTRODUCTION

For decapod crustaceans in general, mechanisms which control recruitment to commercially fished populations remain largely unknown. For most decapods, both density-independent and density-dependent factors have been suggested as potential causes of recruitment variability. Recent reviews of this topic (Jamieson 1986; G. P. Ennis, this volume) have suggested that density-independent processes may be more important during larval development, whereas density-dependent processes are more important after settlement (juveniles). However, environmental effects may influence recruitment at any life history stage from larval to prerecruit (defined here as that stage immediately before moulting to commercial size). For this reason, and because of associated changes in mode of life, density-independent effects will be considered separately for larval, juvenile, and prerecruit stages.

The mechanisms whereby density-independent processes might control recruitment or annual catch fluctuations are inconclusive for *Chionoecetes* spp. and other decapods. Therefore this paper attempts not to draw firm conclusions but to review environmental factors implicated as affecting recruitment in a density-independent manner for *Chionoecetes* and other decapods to serve as a basis for further discussion.

Larval recruitment processes

There have been no studies on the effect of temperature *per se* on recruitment variability in crab populations. However, it has been demonstrated that at Boothbay Harbor, Maine, landings of American lobster (*Homarus americanus*) were significantly correlated with mean annual temperature between 4 and 8 yrs earlier (Flowers and Saila 1972; Dow 1977, 1978). Caddy (1979) concluded that larval survival was related to temperature in that at low ambient temperatures, larval moulting from stage IV to stage V may be delayed indefinitely. He also showed that survival rates were higher for larvae hatched early in the season than for those hatched later. Such an effect is also possible for planktonic larvae of *Chionoecetes*.

Freshwater runoff has also been shown to be correlated with American lobster landings in the Gulf of St. Lawrence (Sutcliffe 1973; Ennis 1986). Lobster landings at Quebec and Prince Edward Island were correlated with spring St. Lawrence River discharge 9 and 8 years earlier, respectively, suggesting that river discharge may have affected larval growth or survival. Sutcliffe (1973) also found a correlation between larval lobster abundance and same-year, June runoff from the Miramichi River. Through a variety of factors, freshwater runoff affects physical oceanographic characteristics, primary production and plankton dynamics (Bugden et al. 1982; Ennis 1986). Therefore freshwater runoff might affect the larval environment of snow crab populations and it could have an effect on annual recruitment levels. Such a potential influence may particularly affect snow crab populations in the Gulf of St. Lawrence.

The most important density-independent factor affecting recruitment in crab populations appears to be currents and circulation features. Broad dispersal of larval stages is characteristic of most crab populations and, for the few species which have been extensively studied, advection of larvae appears to have a pronounced effect on settlement in fishery areas or fluctuations in annual catch.

Cyclic trends in catch of Dungeness crab (*Cancer magister*) between northern California and Washington have been correlated with a variety of factors including upwelling, sunspots and density-dependent processes (reviewed by Botsford 1986a). However the effects of these in controlling catch trends have been discounted because they are either not cyclic or controlling mechanisms are not evident. It is currently felt that southward spring wind stress and density-dependent processes act together in controlling recruitment variation (Johnson et al. 1986; Botsford 1986a, 1986b). Southward wind stress is correlated with catch trends 4-5 years later, is cyclic, and has a reasonable biological interpretation. It has been proposed that larvae are swept north and offshore during the early larval period by the Davidson Current, and are subsequently transported southward and onshore by wind-induced currents. Settlement in favorable areas along the coast would depend on southward wind transport, explaining the high variability in catches in more southern areas. This proposed mechanism is consistent with inverse relationships described by Wild (1980) and Woelke (1971) between crab catch and sea surface temperature 4 yrs earlier. High sea surface temperatures may reflect a relatively strong Davidson Current and weak California Current and therefore a greater net northward transport during larval development (Botsford 1986a).

Larval transport mechanisms are also believed to be of paramount importance in regulating recruitment in estuarine populations of blue crab (*Callinecetes sapidus*) of the Middle Atlantic Bight (Sulkin and Epifanio 1986). Such mechanisms are believed to be complex, involving residual, tidal, and episodic wind-induced circulation in estuaries; the general coastal circulation; and behavioral adaptations of larval stages. Spawning occurs near the mouth of estuaries and zoeae are rapidly exported to shelf waters by surface residual circulation and tidal transport. The degree to which larvae are retained within the Middle Atlantic Bight depends on seasonal reversal of wind-driven, near-shore currents so that loss to the Gulf Stream is prevented. Megalopae may be transported shoreward by deep residual drift or at surface by fortuitous wind events. Sulkin and Epifanio (1986) proposed that while most megalopae are found at the surface, a consistent proportion may be transported at depth by residual drift. They further postulated that transport into estuaries would be enhanced if tidal currents were exploited by larval remaining near the bottom during ebbing tides and rising in the water column during flooding tides. While mechanisms of transport from the shelf to estuaries are uncertain, it is clear that larval development occurs outside estuaries and survival to settlement likely depends on the degree to which coastal circulation features retain larvae within the Middle Atlantic Bight.

In *Chionoecetes*, no density-independent effects of currents during larval development on subsequent recruitment have been conclusively demonstrated, perhaps partly because time series of fishery data and larval distribution studies are not extensive. However such effects appear to be important in other crab species and there is some evidence to suggest their existence in snow crab populations.

Larval *Chionoecetes* appear to be concentrated in surface or near surface waters (Ennis 1983; Kon 1982; Incze et al. 1987), although megalopae may occur at greater depths (Kon 1982). Therefore, larvae may be advected by wind-induced and other circulation features. However, the degree of larval dispersal depends on characteristics of local oceanographic regimes. For example, in the Japan Sea, upwelling areas off Wakasa Bay (Kon 1982) and Honshu (Fukataki 1969; Ito and Ikehara 1971 - cited by Kon 1982) are associated with retention of larvae near the parent population. However off Tottori Prefecture, zoeae were collected in areas distant from the parent population and it was suggested that they had been advected by the Tsushima Current (Kon 1982). In Newfoundland, Ennis (1983) reported that *C. opilio* larvae were collected nearshore only during periods of onshore wind, whereas the parent population was located off the coast at about 165 m depth. Incze et al. (1987) concluded that in the southeastern Bering Sea, larval advection was not an important factor in affecting observed levels of larval abundance.

Studies on the Nova Scotian Shelf (Davidson et al. 1985; Roff et al. 1986) have suggested that snow crab larvae may be transported great distances. Zoeae were most concentrated off eastern Cape Breton Island, whereas megalopae were limited to southwestern Nova Scotia and outer regions of the Bay of Fundy (Roff et al. 1986). It was suggested that these larvae were from the eastern Cape Breton Island population and that longshore larval drift could represent a potential large loss of recruits to that population. It was further proposed that the recent collapse of the eastern Cape Breton Island crab fishery might be related to sustained fishing pressure and a lack of endemic recruitment (Davidson et al. 1985). Recruitment to that population might normally be low, originating from western Cape Breton Island (Davidson et al. 1985; Elner and Bailey 1986). Assuming that larval development requires about 71 days (Davidson et al. 1985), larval exchange among fishing areas seems possible (Davidson et al. 1985; Elner and Bailey 1986). It is noted, however, that the collapse of the eastern Cape Breton Island fishery may also reflect normally low production if this fishing ground, located at the southern edge of commercial snow crab concentrations in the Atlantic, represents a marginal habitat (Elner and Bailey 1986).

Sea ice may also affect recruitment of *C. opilio elongatus* in the eastern Bering Sea, and larval survival may be enhanced by a spring bloom of phytoplankton initiated by sea ice (Somerton 1982). This contention was supported by the observation that recruitment magnitude appears to decrease directly with latitude, as would be expected if an ice edge bloom is important. Further support was indicated by the similarity between the southern extent of sea ice and the distribution of C. opilio. He also found that ice cover in years of high larval survival was greater than in years of low larval survival. However, the case for such a relationship seems weak, since the correlation was significant only at the 10% probability level and was based on a time series of only 11 years, with high larval survival in only 3 years. Furthermore, C. opilio elongatus occurs in areas of the Japan Sea (Watson 1969), which are always ice free.

Factors affecting juveniles

The habitat, migrations and factors affecting survival between settlement and the prerecruit stage are also not well known for Chionoecetes. In the Japan Sea, C. opilio juveniles up to the sixth moulting stage were widely distributed over depths greater than 275 m (Kon 1982). In the Gulf of St. Lawrence, juveniles smaller than 30 mm carapace width (CW) were associated with temperatures below 3°C and depths greater than 60 m (Brêthes et al. 1987). Juveniles ranging from 45-65 mm CW were most abundant at depths of less than 90 m (Coulombe et al. 1985).

Although density-dependent factors are believed to be more important than density-independent factors for juveniles, temperature could conceivably impact indirectly on mortality of juveniles. Low temperature is associated with reduced moulting frequency in lobsters, lined shore crab (Aiken 1980), and blue crab (Leffler 1972). As discussed in the following section, there is also evidence of such an effect in Chionoecetes opilio. Reduction of moulting frequency in snow crab juveniles would delay their subsequent recruitment and increase the period of time during which they might be exposed to density-dependent sources of mortality.

Factors affecting prerecruits

Temperature may have a direct effect on recruitment by delaying the moulting of prerecruits. D. Taylor (Science Branch, P.O. Box 5667, St. John's, Nfld., A1C5X1, unpub. data) suggests that the collapse of a snow crab fishery in Newfoundland may have been the result of low recruitment, caused by low bottom temperatures reducing normal moulting activity. He found that since 1982, the decline in the relative proportion of new shelled crab (which indicates recent moulting) in the offshore Avalon Peninsula area was correlated with a significant decrease in bottom water temperature. Data is limited, but that such a relationship may not be spurious is suggested because when bottom temperature rose briefly in July, 1984, there was a subsequent increase in new shelled crab.

CONCLUSIONS

Data available are inadequate to conclusively reject the hypothesis that density-independent factors have no impact on level of annual recruitment to commercial snow crab fisheries. A variety of environmental factors may affect recruitment, and processes suggested are advection of larvae from fishery areas and a reduction of moulting because of low bottom temperatures. Both of these processes have been implicated as possible causes of Canadian Atlantic snow crab fishery collapses in recent years.

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C. Modelling a Snow Crab Population

Generic Dynamic and Productions Models for Snow Crab

by R. Mohn

INTRODUCTION

The purpose of the following study is to introduce a pair of models to aid in the discussion of snow crab biology and management. These models are constructed to allow a synthetic examination of biological information and harvesting strategies. The author is not familiar with this species and thus the model has been made as general as is reasonable (generic) in order that it may incorporate a wide range of biological facts, beliefs or assumptions. The biological basis for the model is founded on a brief discussion with Dr. R. Elner, to whom all biological reality in the simulation must be credited.

Two basic and related models are developed. One is a dynamic model which is produced so that the stability and periodicity of the modelled system may be investigated. The second is an equilibrium model which produces either yield per recruit results or production estimates, depending on a control parameter. The first model could be run until steady state and yield the same results as the second. However, this would be very inefficient in terms of computer time and assumes the existence of a steady state.

METHODS

The basic life cycle of the modeled system has three components: reproduction, harvest and growth/aging. These will be described in turn with emphasis on both the present configuration and the range of alternates. The simulation has five moult-classes for males >70 mm carapace width (CW). The mean size of each moult-class is 75, 90, 108, 130, and 156 mm CW and the respective weights are .15, .27, .48, .85, and 1.52 kg (length/weight relationship from Bailey 1978). Each age class is comprised of terminal and non-terminal moult animals. There are five age classes of females, all in a single moult-class. The age of recruitment is the age of entering the first moultclass >70 mm CW. The main programs are written in APL and are included at the end of this paper. INIT intializes the descriptive parameters. RUN is the dynamic model. ERUN is the equilibrium model which calls the subroutine STAB which determines the stable size distribution of males under given mortality and moult probabilities. Several of the more important variable names from the simulations are included in the following. They are written in capital letters.

Each simulated year in the dynamic model begins by assessing the reproductive contribution of the stock. The number of reproductive males is determined from a size ogive (MOG). The number of virgin females is set by females is the number surviving from the previous year, plus the recruits. This number is decreased by an exponential function of the male/female ratio. The juvenile production is the product of the nonvirgin females and a fecundity ogive (FOG) whose current value is 1, 1, .5, 0, and 0. The decreasing ogive reflects female senility. The juveniles and the standing stock determine the number of prerecruits through a density dependent term. Trial runs used a density dependency such that the carrying capacity is only in terms of the youngest animals over 70 mm CW. The prerecruits then enter a delay and appear 3 years later as recruits.

The catch is found from the standard catch equation with a partial recruitment and time series of effort. The partial recruitment used in trial runs was 0, .2, 1, 1, and 1. The dynamic model reports catches in numbers of males, while the production and yield per recruit, Y/R, results give the weight of the catch.

Growth is modelled as moults, with increases in size of 20% per year. The probability of moulting (PMO) is in general a function of size, and the trial runs use .8 for all sizes. The number moulting is the product of the fraction moulting and the number of nonterminal males in each moultclass. The remainder are the new terminals. The moulted animals are put into their new moult-class after survivorship is estimated. Instantaneous natural mortality (M) is set at .2 for all sizes and ages. The recruits, with a 1:1 sex ratio, are then added to the population. The females are in a single moult-class but they have an age structure. This age structure was introduced to model senescence among females. At year end, the females are advanced one age class. This completes the annual cycle, which is repeated for the duration of the simulation.

The equilibrium model uses the same descriptive relationships as the dynamic model described above, with a few exceptions. Because this is an equilibrium model, the lag is removed. Also, to facilitate the computations, stable age and size distributions are found analytically for males and females. The equilibrium populations are estimated from eight iterations of a successive approximation procedure. Convergence criteria were not employed and simulations which are far from the initial estimates may not have completely converged, e.g. production runs with instantaneous fishing mortality F=1.5. The equilibrium simulation program has two modes, either Y/R with constant recruitment or a production model with recruitment as described in the dynamic model. The mode is selected by a control parameter (SRON) which turns on or off the stock-recruit relationship.

RESULTS

A series of trial runs were performed to assure internal consistency and to demonstrate the characteristics of the models. Results from dynamic runs are given in Tables 1 and 2 and Figures 1 and 2. The tables contain columns for gamete production, prerecruits, number of virgin females, number of newly moulted, or white, males (considered newly moulted for the full year after moulting), total numbers of males and females above 70 mm, and finally, the numbers of legal hard shell males caught. The average of the variables for years 6 through 40 is included for comparison with the equilibrium runs. The first 5 years are excluded to reduce the effects caused by assumptions on the initial populations which are needed to start the simulations. The first table (and figure) are with a low fishing mortality, .3, white the second is for the higher level of .7. In both cases the results are quite similar and display a 5 year periodicity. As expected the extrema of the catch series are greater when the fishing mortality is higher, but not to a significant degree.

Three equilibrium model runs are reported in Tables 3-5 and Figures 3-5. Table 3 and Figure 3 contain results from a yield per recruit estimation. The plateau of the yield is seen to be fairly stable as F increases above F_{max}.

The production runs in Tables 4 and 5 are essentially Y/R with a stock-recruit relationship added in. Table 4 assumes that all males are reproductive while Table 5 assumes that only 20% of the smallest moultclass is reproductive, 50% of the second, 80% of the third, and all of the 4th and 5th moult-classes. The same simulations are shown in Figures 4 and 5 but the scales have been normalized to make comparison easier with Figure 3. The male biomass is normalized so that 201 is the virgin biomass in all cases. The yield is normalized so that the yield is the same in all cases when F=.7. As expected the results in Figures 3 and 4 are almost identical. This is because the removal of the males has almost no effect when all males are reproductive. An additional run, which is not included in tabular form, was made in which the male partial recruitment ogive was biased further towards older animals, i.e. 0, .3, .7, 1, and 1, and in this case the stock collapsed for F's above .7.

When the average values from the dynamic model runs (Tables 1 and 2) are compared with the equilibrium model values (Table 4), it is seen that dynamic model averages tend to be lower than the equilibrium model values.

DISCUSSION

Two models have been developed to examine the consequences of various harvesting strategies. These models have not been rigorously "fit" to biological data and are not predictive in the usual sense. The first reason for developing the model is to provide a tool to be used by crab biologists. The second use is to examine the characteristics of a synthetic crablike species. The characteristics of such models have not received much attention and are of theoretical interest. However, arguments may be made by analogy between the real and synthetic systems and inferences drawn.

The trial runs showed that the reproductive success of the (synthetic) stock is very resilient if all males are functionally reproductive. A periodicity of about 5 years also was not affected by changing the harvest rate. Assumptions about the characteristics of the density dependence have a strong affect on the magnitude and duration of the cycles. If abundance of prerecruits determines subsequent recruitment, the recruitment pulses are very strong with a five year period. If all animals affect it, as in classical production models, the period increases to 11 years and the recruitment does not stray so far from the mean. The assumptions about the nature of density dependent reproduction are seen to strongly affect the periodicity of recruitment and subsequent yield.

As mentioned in the results section, assumptions about the size of reproductive success for males strongly influence the resilience of the stock to exploitation. The strategy of harvesting only larger males is very stable to high exploitation in terms of yield per recruit.

The dynamic model employs time increments of one year. Therefore, it is not possible to investigate events which happen within the fishing season. It is probable that a complete analysis of such dynamics would require a spatially heterogeneous model. The work required to include spatial effects within our production model is felt to be considerable.

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Table 1. Simulations of numbers of individuals from the dynamic model with F = .3. White refers to the number of males that moulted that year.

Year	Juvenile production	Prerecruits	Recruits	Virgin females	White males	Males > 70mm	Females > 70mm	Male catch >95mm
1	1704	1022	200	5	247	520	520	118
2	1204	651	200	6	188	478	509	128
3	848	440	1022	7	162	432	490	101
4	2416	0	651	31	419	820	879	87
5	3058	0	440	15	453	947	911	128
6	2602	0	0	11	390	951	929	188
7	1157	780	0	0	206	703	724	187
8	295	216	0	0	98	498	556	144
9	0	0	780	0	36	324	267	80
10	1530	0	216	9	266	608	489	44
11	1702	499	0	2	228	579	427	76
12	877	649	0	0	120	453	350	113
13	145	114	499	0	58	327	287	85
14	972	0	649	13	192	482	484	54
15	2079	0	114	10	318	679	577	59
16	1620	780	0	2	217	590	490	111
17	622	463	0	0	110	445	401	119
18	77	60	780	0	54	316	328	82
19	1516	0	463	16	276	603	567	47
20	2178	0	60	7	312	692	576	75
21	1399	816	0	1	190	573	481	127
22	409	306	0	0	95	422	394	114
23	41	32	816	0	46	298	323	75
24	1591	0	306	13	281	603	529	39
25	1934	224	32	4	267	621	501	75
26	1112	737	0	1	152	503	415	120
27	258	199	224	0	75	365	340	97
28	462	168	737	6	110	371	390	63
29	1802	0	199	11	295	627	538	46
30	1745	569	168	3	237	590	483	90
31	1150	465	0	3	178	539	474	117
32	409	311	569	0	94	395	388	97
33	1219	0	465	14	229	564	561	70
34	1837	0	311	7	280	648	556	74
35	1749	164	0	5	255	658	574	112
36	821	588	0	0	135	494	439	120
37	209	160	164	0	66	358	360	95
38	325	157	588	2	79	323	272	54
39	1420	0	160	8	233	526	431	40
40	1388	602	157	2	187	490	376	72
Avg*	1104	259	242	4	182	521	465	90

*The average is over years 6 to 40.

Table 2. Simulations of numbers of individuals from the dynamic model with F = .7. White refers to the number of males that moulted that year.

Year	Juvenile production	Prerecruits	Recruits	Virgin females	White males	Males > 70mm	Females > 70mm	Male catch >95mm
1	1704	1022	200	5	220	520	520	166
2	1200	649	200	8	148	439	509	138
3	842	437	1022	11	129	368	490	96
4	2393	0	649	39	392	756	879	81
5	3044	0	437	18	420	895	910	166
6	2584	0	0	13	331	883	927	213
7	1149	776	0	1	142	601	722	187
8	293	215	0	0	46	381	554	113
9	0	0	776	0	13	229	266	52
10	1507	0	215	14	257	540	486	25
11	1689	502	0	3	215	533	425	102
12	872	646	0	0	87	404	348	120
13	144	114	502	0	28	257	285	69
14	964	0	646	19	174	414	484	33
15	2069	0	114	12	307	637	577	72
16	1614	780	0	2	188	552	489	138
17	619	461	0	0	70	385	401	116
18	76	60	780	0	23	239	328	61
19	1500	0	461	22	262	542	567	28
20	2168	0	60	8	297	653	575	102
21	1394	815	0	1	153	530	480	147
22	407	305	0	0	55	531	393	103
23	40	32	815	0	18	219	322	52
24	1574	0	305	18	271	548	528	23
25	1926	229	32	5	252	585	500	105
26	1108	735	0	1	117	461	414	133
27	257	198	229	0	41	297	339	83
28	465	166	735	11	88	301	392	42
29	1795	0	198	15	286	583	539	45
30	1741	570	166	3	216	556	484	119
31	1139	468	0	4	140	489	473	122
32	404	307	570	0	59	323	387	88
33	1206	0	468	20	205	496	560	51
34	1836	0	307	10	264	601	557	88
35	1742	177	0	7	223	612	573	129
36	816	585	0	0	97	431	439	123
37	206	158	177	0	32	281	359	76
38	347	159	585	5	67	263	278	35
39	1425	0	158	10	227	484	434	37
40	1385	605	159	2	172	459	378	95
Avg*	1099	259	242	6	155	461	465	89

*The average is over years 6 to 40.

Table 3. Yield (numbers) per recruit, with constant recruitment and the number of reproductive males determined from the size ogive (MOG) = 1, 1, 1, 1, and 1. White refers to the number of males that moulted that year.

F	Juvenile production	Prerecruits	Virgin females	White males	No. Males > 70mm	No. Females > 70mm	Yield (number)
.00	848	200	5	172	201	349	0
.05	845	200	7	172	178	349	22
.10	842	200	8	172	161	349	32
.15	839	200	9	172	149	349	36
.20	836	200	10	172	139	349	37
.25	834	200	11	172	131	349	38
.30	832	200	12	172	125	349	37
.35	830	200	13	172	119	349	36
.40	828	200	14	172	114	349	35
.45	826	200	14	172	110	349	34
.50	824	200	15	172	106	349	33
.55	823	200	16	172	103	349	32
.60	821	200	16	172	99	349	31
.65	820	200	17	172	97	349	30
.70	819	200	17	172	94	349	29
.75	817	200	18	172	92	349	28
.80	816	200	18	172	90	349	27
.85	815	200	19	172	88	349	27
.90	814	200	19	172	86	349	26
.95	813	200	20	172	85	349	25
1.00	812	200	20	172	83	349	25
1.05	811	200	20	172	82	349	24
1.10	810	200	21	172	81	349	23
1.15	809	200	21	172	80	349	23
1.20	808	200	21	172	78	349	22
1.25	808	200	22	172	77	349	22
1.30	807	200	22	172	76	349	21
1.35	806	200	22	172	76	349	21
1.40	805	200	23	172	75	349	21
1.45	805	200	23	172	74	349	20
1.50	804	200	23	172	73	349	20

Table 4. Yield per recruit, with variable recruitment and the number of reproductive males determined from the size ogive (MOG) = 1, 1, 1, 1, and 1.

F	Juveniles	Prerecruits	Virgin females	White males	No. Males > 70mm	No. Females > 70mm	Yield (number)
.00	1479	347	7	226	264	459	0
.05	1471	346	9	226	234	459	38
.10	1464	345	11	226	212	458	54
.15	1458	345	12	226	196	458	62
.20	1453	345	13	225	183	458	64
.25	1448	344	15	225	172	458	65
.30	1443	344	16	225	163	457	64
.35	1439	343	17	225	156	457	63
.40	1435	343	18	225	149	457	61
.45	1431	343	19	225	144	457	59
.50	1427	342	20	225	139	456	57
.55	1424	342	20	225	134	456	55
.60	1421	342	21	224	130	456	53
.65	1418	342	22	224	126	456	51
.70	1415	341	23	224	123	456	50
.75	1412	341	23	224	120	455	48
.80	1410	341	24	224	117	455	47
.85	1407	341	25	224	115	455	45
.90	1405	340	25	224	113	455	44
.95	1402	340	26	224	111	455	43
1.00	1400	340	26	224	109	455	42
1.05	1398	340	27	224	107	455	41
1.10	1396	340	27	224	105	454	40
1.15	1394	339	28	224	104	454	39
1.20	1393	339	28	224	102	454	38
1.25	1391	339	28	224	101	454	37
1.30	1389	339	29	224	100	454	36
1.35	1388	339	29	223	98	454	36
1.40	1386	339	30	223	97	454	35
1.45	1385	339	30	223	96	454	34
1.50	1383	338	30	223	95	454	34

Table 5. Yield per recruit, with variable recruitment and the number of reproductive males determined from the size ogive (MOG) = .2, .5, .8, 1, and 1.

F	Juveniles	Prerecruits	Virgin females	White males	No. Males > 70mm	No. Females > 70mm	Yield (number)
.00	1296	330	50	220	258	448	0
.05	1246	324	61	219	226	444	36
.10	1202	320	71	217	204	441	50
.15	1164	315	79	216	187	438	56
.20	1130	311	86	214	174	435	58
.25	1099	308	92	213	163	432	58
.30	1071	304	97	212	154	430	57
.35	1044	301	102	211	146	428	55
.40	1020	298	106	209	139	425	53
.45	998	295	110	208	133	423	51
.50	976	292	113	207	128	421	49
.55	956	289	117	206	123	419	47
.60	938	286	120	205	119	217	45
.65	920	284	122	204	115	415	43
.70	903	281	125	204	112	414	41
.75	887	279	127	203	109	412	39
.80	872	277	129	202	106	410	38
.85	857	274	131	201	103	408	37
.90	843	272	133	200	101	407	35
.95	830	270	135	199	99	405	34
1.00	817	268	136	199	96	404	33
1.05	805	266	138	198	95	402	32
1.10	793	264	139	197	93	401	31
1.15	782	262	141	197	91	399	30
1.20	771	260	142	196	89	398	29
1.25	760	258	143	195	88	396	28
1.30	750	257	144	194	87	395	28
1.35	740	255	145	194	85	394	27
1.40	731	253	146	193	84	392	26
1.45	722	252	147	193	83	391	25
1.50	713	250	147	192	82	390	25

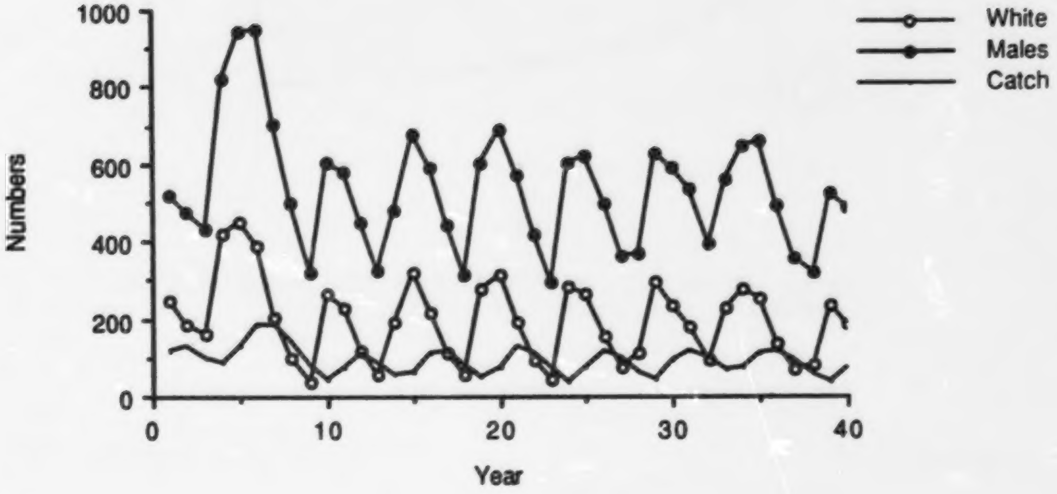

Figure 1. Forty year simulation with light (F=.3) fishing pressure. The solid line is catch in numbers, the open circles are the number of newly molted animals (white crabs) and the solid circles are the total number of males >70mm.

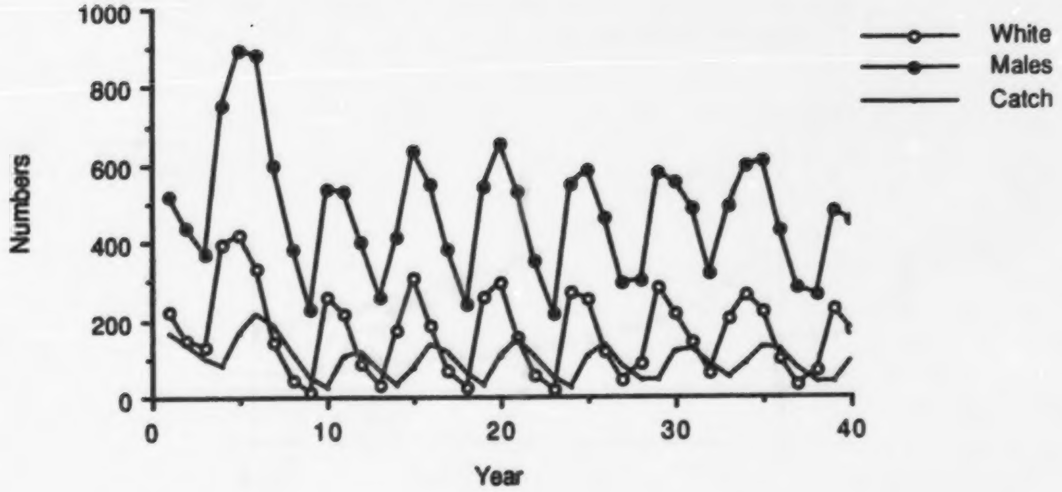

Figure 2. Forty year simulation with heavy (F=.7) fishing pressure. The solid line is catch in numbers, the open circles are the number of newly molted animals (white crabs) and the solid circles are the total number of males >70mm.

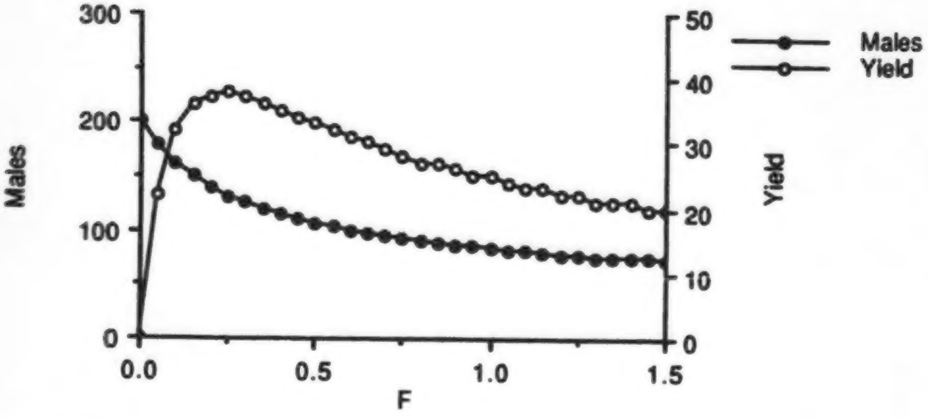

Figure 3. Traditional yield per recruit for snow crab. The open circles are yield and the closed circles are male (>70mm) biomass.

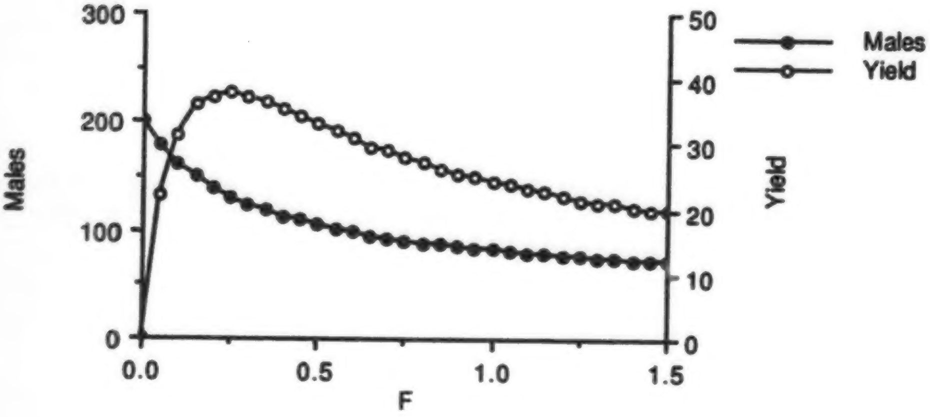

Figure 4. Joint yield per recruit and stock recruit analysis for snow crab. All males are fully reproductive.

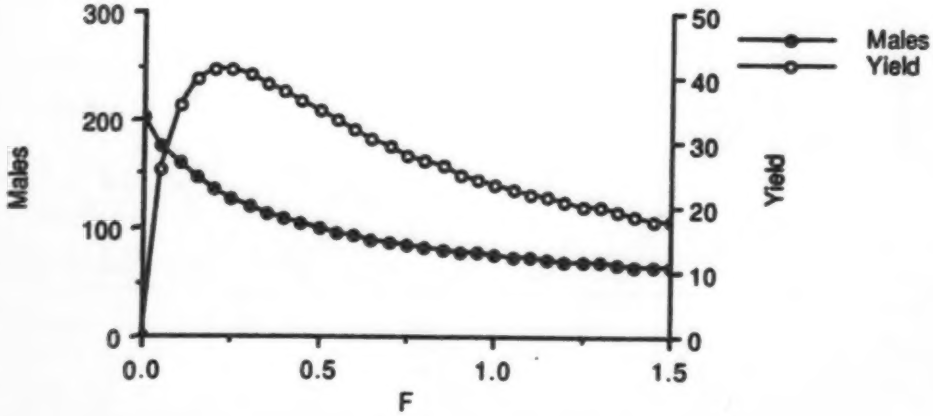

Figure 5. Joint yield per recruit and stock recruit analysis for snow crab. The male reproductivity ogive is .2 .5 .8 1 1.

Listing of principal routines.

Routine RUN

```
RUN
STATS← 0 8 ρP←((ρPIN),1+NY)ρY←FV←0
P[;;1]←PIN
NT←P[;1;1]×1-PMO ⍝ INITIALIZE TERMINAL MOLT GROUP
LAG←NLAGρ+/PIN[1;]
YLOOP:→(NY<Y←Y+1)/END
ZZ←(1-*-ZK)÷ZK←M+(FK←EF[Y]×SEL),[1.5]0
NREM←MOG+.×T←P[;1;Y] ⍝  NUMBER REPRODUCTIVE MALES
NV←(FV×+/1↓U)+1↑U←P[;2;Y] ⍝ NUNBER VIRGIN FEMALES NEW + OLD V'S
NV←NV×*-3×(NREM)÷+/U ⍝RATIO OF MALES TO FEMALES DECREASES VIRGINS
FV←NV÷+/U ⍝FRACTION VIRGINS AMONG FEMALES
GAM←(FOG+.×U)×1-NV÷+/U ⍝ GAM PRODUCTION
NSPIN←0⌈NSPIN-0⌈NREM-NREF ⍝ NUMBER OF SPINSTERS FOR NEXT YEAR
PREC←0⌈GAM×(1-(DDF+.×+/P[;;Y])÷CC) ⍝ DENSITY DEPENDENT TERM
LAG←PREC,¯1↓LAG ⍝  PUT PRERECRUITS INTO DELAY
C←FK×T×ZZ[;1]÷ZK[;1] ⍝ CATCH EQUATION ON MALES
T←T×*-ZK[;1] ⍝  MALE SURVIVORSHIP
NT←NT×*-ZK[;1] ⍝  SURVIVORSHIP OF THE TERMINAL GROUP
NWC←+/NM←(T-NT)×PMO ⍝ NUMBER MOLTING IS NON-TERMINAL TIMES RATE
NT←T-NM ⍝   NUMBER TERMINALIS TOTAL - NUMBER MOLTED
P[;1;Y+1]←NT+0,¯1↓NM ⍝  NEW SIZE DISTRIBUTION FOR NEXT YEAR
P[;2;Y+1]←0,¯1↓U×*-ZK[;2] ⍝ ADVANCE FEMALES TO NEXT SENESCENCE STAGE
P[1;;Y+1]←P[1;;Y+1]+0.5×NEWS←¯1↑LAG ⍝ ADD RECRUITS, 50-50 SEX RATIO
STATS←STATS⍪GAM,PREC,NEWS,NV,NWC,(+⌿P[;;Y]),+/C
→YLOOP
END:MNEC ECHO HEAD
MNEC ECHO 0 ROUND STATS[NY;]
```

Routine ERUN

```
ERUN
NF←ρFR←' FISHING MORTALITY RANGE ' DEFAULT FR
SRON←'STOCK-RECRUIT ON? 0-1 ' DEFAULT SRON
STATS← 0 8 ρF←0
FLOOP:→(NF<F←F+1)/END
ZZ←(1-*-ZK)÷ZK←M+(FK←FR[F]×SEL),[1.5]0
T←ZK[;1]STAB PMO ⍝ STABLE SIZE DISTRIBUTION OF MALES
U←100×*-+\0,¯1↓ZK[;2] ⍝ STABE AGE DISTRIBUTION.FEMALES
NREM←MOG+.×T ⍝  NUMBER REPRODUCTIVE MALES
NV←(+/U)×*-3×(NREM)÷+/U ⍝RATIO OF MALES TO FEMALES DECREASES VIRGINS
UT←U+I←0 ⍝  TRIAL FEMALE SPECTRUM  U
TOP:→(8<I←I+1)/BOT
GAM←(FOG+.×UT)×1-NV÷1⌈+/UT ⍝ GAM PRODUCTION
PREC←0⌈GAM×(1-(DDF+.×+/(T×UT÷U),[1.5]UT)÷CC) ⍝ DENSITY DEPENDENT TERM
PREC←(200,PREC)[1+SRON]
UT←UT×(0.5×PREC÷1E¯3⌈UT[1])*0.5
→TOP
BOT:C←FK×T×(FF←UT÷U)×ZZ[;1]÷ZK[;1]
STATS←STATS⍪FR[F],FF[1]×GAM,PREC,NV,NWC,(+/T×WAA),(+/U×WAA),C+.×WAA
→FLOOP
END:MNEC ECHO '     F   GAM   PREC   NV   NWC  MALES FEMALES YIELD '
MNEC ECHO 1 ROUND STATS
```

Subroutine STAB

```
Z←M STAB PM;A;B;IN;S;E
⍝CASCADE OF STABLE MOULT CLASSES
IN←100
A←IN×*-+\M
B←A××\1,¯1↓PM ⍝ INFLUXES TO EACH GROUP
S←(B×1-PM)÷1-*-M ⍝ STANDING STOCK TO BALANCE TERMINALS INFLUX
Z←S+E←A××\PM ⍝ E IS EFLUX VECTOR (MOLTING OUT)
⍝ 3 ROUND⍉ 3 5 ρZ,S,E
Z←Z×*M
```

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